Assessing Calf Survival and the Quantitative Impact of Reproductive Success on the Declining Moose (*Alces alces*) Population in Northeastern Minnesota

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Dedication

I dedicate this dissertation to my wife, Lisa Raetz, and our growing family, including new addition Charles “Charlie” Raetz Severud (born just days before this dissertation was defended).

Abstract

Ungulate reproductive success is an important driver of population performance. Long-term, the northeastern Minnesota moose (*Alces alces*) population declined 58% since 2006, yet aerial survey estimates indicate stability during 2012–2017. Because causal mechanisms for this decline were largely unknown, I investigated calf production, survival and cause-specific mortality of calves of global positioning system (GPS)-collared dams of this population. Global positioning system collars have been deployed on adult moose and other ungulates to study various aspects of their ecology, but until the current study they had not been fitted to moose neonates. In 2013 and 2014, I GPS-collared 54 neonates and monitored them for survival. In 2015, I monitored 50 calving dams for signs of neonatal mortality using behavioral cues, and assessed seasonal calf survival with aerial surveys. In 2013 and 2014, collared calf survival to 9 months was 0.34 (95% CI = 0.23–0.52), whereas uncollared calf survival in 2015 was estimated at 0.40 (95% CI = 0.30–0.54). Survival in all 3 years dropped dramatically in the first 50 days of life; hazard peaked at about 15 days of age when dams and calves departed calving sites. Predation was the leading cause of death of collared calves (84% of mortalities); wolf (*Canis lupus*) predation accounted for 77% of deaths. The cumulative probability of succumbing to all forms of mortality by 9 months of age was 69.8%. I documented higher wolf predation than other recent studies with similar predator communities.

Habitat use during calving and the energetically demanding post-parturition period can be an important determinant of neonatal survival. I surveyed and compared

habitat characteristics of pre-calving, calving, peak-lactation, and mortality sites at a fine and broad scale. I also compared mortality sites of calves killed by wolves versus other causes, as well as calving sites of cows that successfully reared a calf to winter to those that did not. Cows tended to move to areas of more conifer forest cover to calve. During peak-lactation, cows and their calves used steeper areas with abundant forage, high concealment, and less conifer cover. Mortality sites were more level than other site types. Generally, wolf-kill sites were farther from roads. Cows that successfully reared a calf to winter typically calved in areas with more deciduous forest and less forested wetland cover than cows whose calves died.

I estimated population growth rate (λ) using adult survival and calf recruitment data from the Minnesota Department of Natural Resources demographic studies and the Recruitment-Mortality (R-M) Equation, and compared this estimate to those calculated using data from the annual aerial survey. Measures of recruitment were similar whether derived from the survey or collaring studies, but generally were higher in the collared sample. More recent calculations of λ (derived from the survey [2012–2017 stabilization; 1.02 ± 0.16 (SE)] and using the R-M Equation [1.04 ± 0.04]) indicated growth over the next 50 years. However, the stochastic model using parameters from the adult and calf studies indicated an average decline in the population over the next 50 years ($\lambda = 0.94 \pm 0.004$).

Habitat improvement projects for moose should consider not only forage requirements, but also cover, slope, and road density. Identifying specific causes of calf mortality and understanding their relations to various landscape characteristics and other

extrinsic factors should yield insight into mechanisms contributing to the declining moose population in northeastern Minnesota and serve as a basis for ecologically sound management responses.

Table of Contents

List of Tables

List of Figures

Chapter 1: Using GPS Collars to Determine Parturition and Cause-specific Mortality of Moose Calves

ABSTRACT Global positioning system (GPS) collars have been deployed on adult moose (*Alces americanus*) and other ungulates to study various aspects of their ecology, but until the current study they have not been fitted to moose neonates. The moose population in northeastern Minnesota has been declining since 2006, and information on neonatal survival and cause-specific mortality are needed. I monitored hourly movements of GPS-collared cows for indications of calving. During 2 May–2 June 2013 I observed 47 of 73 collared cows (50 known pregnant, 17 not pregnant, 6 unknown pregnancy status) make "calving movements" followed by a clustering of locations. After allowing a mean bonding time of 40.2 hours, their calving sites were approached and a crew captured and GPS-collared 49 neonates from 31 dams. I closely monitored dam-calf movements and launched rapid investigative responses to calf mortality notifications to determine cause of mortality. Mean response time was 53.3 hours, but ranged from 0.3 to 579 hours, depending on collar accessibility and proper functioning of the GPS component. I censored capture-related mortalities and slipped collars. Twenty-five of 34 calves (74%) died of natural causes as of 31 December 2013, including 1 after natural abandonment, 1 after abandonment of unknown cause, 1 drowning, 1 unknown predator-kill, 1 lethal infection from wolf (*Canis lupus*) bites, 4 black bear- (*Ursus americanus*) kills, 12 wolf-kills, and 4 "probable wolf-kills." As this technology develops, the quantity and quality of survival, cause-specific mortality, movement, and habitat use data generated from intense monitoring of GPS-collared adults and offspring

will have unprecedented value associated with management at the population and landscape scales.

INTRODUCTION

Minnesota's northeastern (NE) moose (*Alces americanus*) population has been experiencing a downward decline from 2006 to 2014 (DelGiudice 2014). The state's northwestern (NW) population fell dramatically from ~4,000 to <100 animals from the mid-1980s to 2007 (Murray et al. 2006, Lenarz et al. 2009). From 2006 to 2014, the northeastern population has exhibited adult annual survival rates similar to those documented for the northwestern population during its decline (81%; Lenarz et al. 2009, M. Carstensen, Minnesota Department of Natural Resources [MNDNR], unpublished data). Lenarz et al. (2009) reported 89% of natural mortalities of collared adults as "unknown cause"; estimated calf survival was 40%, but causes of mortality were not investigated (Lenarz et al. 2010). Furthermore, calves were assumed to have died if their dam died, but this depends on timing of the dam's death relative to the calf's age (Jolicoeur and Crête 1988). Calf survival can markedly affect annual variation in population growth, especially in populations experiencing low and variable survival rates of calves (Gaillard et al. 2000, Raithel et al. 2007, Patterson et al. 2013). Recently, the MNDNR initiated aggressive studies of cause-specific mortality of adult moose and calves in northeastern Minnesota to address information needs and to facilitate a more effective management response to the declining population.

Very high frequency (VHF) collars were deployed in the aforementioned moose survival study (Lenarz et al. 2009, 2010) and others focused on moose calf survival and cause-specific mortality (Ballard et al. 1981, Osborne et al. 1991, Keech et al. 2011,

Patterson et al. 2013). Observations of VHF-collared animals commonly are limited by overall frequency of fix locations (determined from the ground or fixed-wing) and flights biasing locations toward diurnal and fair weather conditions (Rodgers et al. 1996). Consequently, response times to mortality events are delayed. Using VHF collars also is time and labor intensive compared to GPS collars (Moen et al. 1996, Rodgers et al. 1996, Bowman et al. 2000). Global positioning system collars have been used on adult moose to examine habitat use, predation, fine-scale movement, migration, and parturition behavior (Moen et al. 1996, Rodgers et al. 1996, Welch et al. 2000, van Beest and Milner 2013, McGraw et al. 2014, White et al. 2014). I intensively monitored pre-parturient, GPS-collared cows to facilitate GPS-collaring their neonates. Until the current study, expandable GPS collars have not been fitted to moose neonates, and had only recently been used in small numbers on other ungulate neonates in the wild (fallow deer [*Dama dama*], $n = 3$, Kjellander et al. 2012) or in captivity (domestic horse, $n = 4$, Hampson et al. 2010). This technology allowed me to conduct cause-specific mortality investigations in a more timely manner than had been possible with conventional telemetry techniques (Barber-Meyer et al. 2008, Keech et al. 2011, Patterson et al. 2013).

The objectives of this study were to 1) describe the efficacy of using movement behavior of GPS-collared, adult female moose to determine timing and location of calving, facilitate neonate capture, and assess calf production, and 2) evaluate remote tracking of GPS-collared dams and neonates to expedite investigations of calf mortalities and assign cause of mortality with greater confidence.

STUDY AREA

I conducted this study in a 6,636-km^2 area of northeastern Minnesota, located between 47° 00’ N and 47° 56’ N, 89° 57’ W and 92° 17’ W (Fig. 1). The area is characterized as Northern Superior Uplands (MNDNR 2014) and is interspersed with lakes, wetlands, logging roads, and low density human settlements. Stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) predominate the lowlands, and balsam fir (*Abies balsamea*), jack (*Pinus banksiana*), eastern white (*P. strobus*), and red pines (*P. resinosa*) are most prevalent on the uplands, where mixed stands of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) also occur. Open areas include lowland or upland deciduous shrub and sedge (*Carex* spp.) meadows (MNDNR 2014).

White-tailed deer (*Odocoileus virginianus*) populations occur at pre-fawning densities of ≤4 deer/km^2 (MNDNR 2011). Major predators of moose in the area include gray wolves (*Canis lupus*, 3 wolves/100 km^2, Erb and Sampson 2013) and black bears (*Ursus americanus*, 23 bears/100 km^2, Garshelis and Noyce 2011). Moose have not been harvested in the state since 2012 (DelGiudice 2014).

METHODS

Adult Moose Capture and Handling

In January and February 2013, 111 adult moose (84 females, 27 males) were captured and handled as part of the MNDNR’s study of cause-specific mortality (Butler et al. 2013). Capture and handling protocols met American Society of Mammalogists guidelines (Sikes et al. 2011). The capture crew fitted moose with Iridium GPS Plus collars (Vectronic Aerospace GmbH, Berlin, Germany). These collars have an expected life of 5 years and use Iridium satellite 2-way communication technology, which allows

them to be reprogrammed remotely. Collars collected GPS locations every 4 hours 15 minutes and transmitted all recorded locations after 6 successful fixes along with the collar status (Normal or Mortality). When a collar entered mortality mode (triggered by limited motion for 6 hr), the accelerometer triggered a mortality schedule (immediate collection of 10 fixes to force a data transmission, followed by fixes acquired at 30-minute intervals for 6 hr) and a notification was sent to the base station, which then generated both SMS (text message) and email notifications to designated project staff. Alerts listed the collar serial number and time it entered mortality mode. Summer field tests demonstrated mean linear error (± SE, range) of locations from adult collars of 3.7 m (± 0.3, 0–17 m) under open canopy and 7.0 m (± 0.3, 1–36 m) under dense canopy (≥80% closure; W. J. Severud, University of Minnesota, unpublished data).

Minnesota Department of Natural Resources analyzed blood samples taken at time of capture for progesterone concentrations. Previously reported mean progesterone levels of pregnant cows ranged from 6.1 to 7.4 ng/ml, non-pregnant cows 0.4 to 0.7 ng/ml, and 1 male 0.42 ng/ml; the pregnancy threshold was ≥2 ng/ml (Haigh et al. 1982, Testa and Adams 1998, Murray et al. 2006). Serum progesterone indicated a 75% pregnancy rate of all captured cows that we tested, with mean ± SD progesterone levels of pregnant cows, non-pregnant cows, and males of 4.8 ± 1.6 (n = 58), 0.4 ± 0.2 (n = 19), and 0.5 ± 0.7 (n = 23) ng/ml, respectively (E. A. Butler and M. Carstensen, MNDNR, unpublished data).

Monitoring for Calving

I began monitoring 73 cows on 1 May 2013 (50 pregnant, 6 unknown pregnancy status [no blood sample taken at capture], and 17 not pregnant); 11 of 84 collared cows died

between capture and initiation of monitoring (Butler et al. 2013). Female collars were remotely programmed to acquire fixes hourly during May and to transmit 4 times/day. I monitored cow movements during pre-parturition and calving, with particular attention paid to pregnant cows. We looked for movement patterns indicative of calving (Welch et al. 2000), including a long-distance movement followed by localization (Bowyer et al. 1999, Testa et al. 2000*a*, Poole et al. 2007, McGraw et al. 2014). Generally, parturition occurs within 12 hours after localizing (R. A. Moen, Natural Resources Research Institute, personal communication). I received automated reports by email 6 times/day (0400, 0800, 1200, 1600, 2000, 2400 hr). Each email included 2 files describing the most recent location of each animal (in csv and kml formats), in addition to a pdf report displaying movement and location metrics for each collared cow. The reports contained a coarse-scale map of northeastern Minnesota with all cows displayed and a summary table of all animal locations and distances moved in the last 24 and 48 hours. This table was followed by a separate page for each cow that included the date and time of the last location, movement path over the last 5 days, movement path over the last 24 hours overlaid on Google Earth (earth.google.com) imagery, and a plot showing the 3-hour moving average of distances moved per hour (speed) over the previous 10 days. I monitored the distance plot for relatively large peaks in movements followed by a dampening of movement (i.e., localization). If a cow's displacement was <100 m during a 36-hour interval after making a long-distance movement, the program flagged it as "localized," and its calf was determined "eligible" for capture. This gave cows and calves at least 24–36 hours of bonding time. Once reports indicated a localized cow, I checked the movement path using Vectronic's website (www. vectronic-wildlife.com)

and graphed hourly movement rates in Excel (2010; Microsoft Corporation, Redmond, WA) using data sent to our base station and managed by GPS Plus X software (Vectronic Aerospace GmbH, Berlin, Germany). Once the calf was collared, its collar was paired with its dam's collar so that proximity between them could be monitored as well. Calves then had similar reports generated automatically.

Calf Capture and Handling

A capture crew (Quicksilver Air, Fairbanks, AK) located eligible calves via helicopter and then landed to allow 1–2 handlers to disembark. Typically, handlers were able to easily approach and capture calves. Each calf was weighed (± 0.5 kg) by spring-scale, ear-tagged, and blood-sampled. The crew recorded morphological measurements (hind foot length, upper and lower neck circumference, chest girth, total body length [± 1 cm]) and rectal temperature (± 0.1° F), and fitted GPS collars. The crew weighed calves in grain sacks (n = 11), but then switched to using a rope sling to limit transferring scent from 1 calf to another (n = 32). Handlers did not wear gloves. I estimated age of calves (± 0.5 days) following Larsen et al. (1989). I used a fixed-wing aircraft as a spotter plane for the first 5 days of captures to record handling times, dam behavior and status (e.g., percent hair loss due to winter tick [*Dermacentor albipictus*] infestation, aggressiveness). If twins were spotted, both were handled, collared, and released together to minimize the risk of capture-related abandonment (Keech et al. 2011). I placed collars in bags with vegetation, mud, and moisture for ≥24 hours before captures to mask human and collar scent. All calf captures and handling protocols followed requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (Protocol 1302-

30328A) and were consistent with guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011).

Calf Collars

Calves were fitted with a GPS PLUS VERTEX Survey-1 GLOBALSTAR collar (Fig. 3) with expandable belt (420 g, box dimensions 85 × 59 × 75 mm, belt 3 cm wide, initial circumference 35 cm, fully expanded circumference 65 cm; Vectronic Aerospace GmbH, Berlin, Germany), which recorded hourly locations for 1 year and transmitted (via Globalstar satellite 1-way communication) every third successful location. All locations also were stored on-board the collar. These collars were programmed by the vendor and could not be reprogrammed in-hand or remotely. Calf collar accelerometers used similar mortality delay, schedule, and notifications as the adult collars (see above). Text messages included the serial number of the calf's and dam's collar. The expandable collar material included stitched expansion loops and a breakaway section designed to deteriorate at ~400 days. Summer field tests demonstrated that mean linear error (± SE, range) of calf collar locations was 24.9 m (± 2.7, 1–274 m) under open canopy and 33.7 m (± 3.1, 1–236 m) under dense canopy (≥80% closure; W. J. Severud, unpublished data).

Dam-calf Monitoring

Once calves were collared, I monitored dam-calf groups several times daily as updated locations were received by the base station. I examined proximity and synchrony of dam-calf GPS locations until fate was known (mortality, slipped collar, failed collar). When I received a mortality alert text message, a mortality response team initiated an investigation. Collars can be kept in active mode by motion caused by predators,

scavengers, or moving water, and data transmissions can be blocked if satellite reception is poor (e.g., if collar is buried). I decided to rely on closer monitoring of dam-calf groups after I observed several dams moving from stationary calf collars, yet I did not receive a mortality alert text message. I consulted the Vectronic website each morning and reviewed raw data from the base station to see if collars were actively transmitting or were in mortality mode. Collars that stopped transmitting may have been buried. These methods also allowed us to track capture-induced abandonment of calves by their dams (DelGiudice et al. 2015).

Mortality Investigations

To avoid disturbing a dam and any surviving calves, I checked the dam's most recent location before deploying a mortality response team. The dam's location or behavior around the time the calf's collar entered mortality mode could indicate if the alert message was the result of a true mortality or a slipped collar. If a dam remained at the mortality site, I did not deploy a response team until it departed.

I used several sets of coordinates when navigating to a mortality site, including the most recent calf(ves) and dam locations, the locations at the estimated time of death, locations from the past 2 days (to assess whether the collar was moved from a mortality or kill site to its current location), and locations from the last time dam and calf were together. All locations were loaded into handheld GPS units (GPSmap 62sc, Garmin, Olathe, KS).

In addition to relying on GPS location data, I also homed in on VHF frequencies of the presumed dead calf, its dam and sibling (if a twin). Other equipment packed in for mortality investigations included a full field necropsy kit (M. Carstensen, unpublished

data) to be used when the carcass could not be extracted from the field, as well as safety equipment (yellow vests, eyewear, bug suits, bear spray, and 12-gauge shotgun loaded with rubber shot, buck shot, and a slug). Since I was attempting to estimate cause-specific mortality and was alerted to mortalities 6 hours post mortem, I needed to anticipate potentially aggressive predators or scavengers defending fresh kills or carcasses (McNay 2002, Herrero et al. 2011), or dams protecting dead calves (LeResche 1968). Care was taken to haze off predators and scavengers when approaching the mortality site; bear repellent spray and firearms were available as a last resort for protection, but their use was not anticipated (Smith et al. 2008, 2012). I postponed investigations when predators were sighted on the carcass; return was dependent on the age and size of the carcass as an indication of how long the predator or scavenger might feed. Response crews consisted of ≥3 people.

While navigating to the mortality site, I used telemetry to correct for GPS error and confirm the collar was still in mortality mode (96 bpm vs 48 bpm when in active mode). When our team arrived within 100 m of the presumed mortality site, I conducted a safety briefing. We distributed ourselves to optimize search effectiveness, but all group members stayed within earshot or line of sight. We searched for sign indicative of specific predators (e.g., wolves, bears) or of scavenging (Ballard et al. 1979). Characteristics of carcasses preyed upon by bears included peeled or inverted hide, cached body parts, selective feeding of viscera or sensory organs, and claw marks across the body. Wolves typically did not consume viscera (especially the rumen and its contents), chewed the ends of long bones, scattered remains over a large area, and inflicted puncture wounds on the head, neck, or hindquarters. Depredated carcasses

exhibited subcutaneous hemorrhaging at wound sites or were surrounded by signs of a struggle (broken or matted vegetation, blood sprays on vegetation or collar). Scavenged carcasses may be surrounded by many pellets and smell of decay. Sternal or lateral carcass position of older and larger calves also may indicate predation or scavenging, respectively (M. W. Schrage, Fond du Lac Resource Management Division, personal communication). We looked for moose or predator hair, tracks, or scat. Photographs were taken before any evidence was handled. We photographed tracks and scat and collected scat and hair when predator identification was uncertain. Swabs also were available to sample for DNA from predator or scavenger saliva from wounds on the carcass (B. R. Patterson, Ontario Ministry of Natural Resources and Forestry, personal communication). I used the preponderance of evidence to assign causes of mortality.

My primary field objective was to recover the entire carcass and deliver it to the University of Minnesota's Veterinary Diagnostics Laboratory (VDL) for necropsy. When the carcass could not be extracted and transported (as in the case of older or larger calves in remote areas), I conducted a detailed field necropsy. When scavenged or mostly consumed, I collected fresh organ and tissue samples and shipped them to the VDL as feasible (Butler et al. 2011).

Necropsies were thorough whether conducted in the field or at the VDL, although necropsies conducted by board-certified pathologists in a lab setting were more likely to yield detailed results. I scanned for external and internal abnormalities, collected tissue samples (stored fresh and in formalin) from most organs, weighed the carcass, and measured the same morphometrics we recorded at captures. Pathology and histology tests were conducted by the University of Minnesota's VDL and Clinical Pathology

Laboratory. When the cause of death was unknown, I collected various samples for metagenomic testing (M. Carstensen, personal communication). I checked stomachs for curdled milk or vegetation, which depending on a calf's age, could yield insight into whether it was abandoned, refused milk by its dam, or unable to nurse. Pathologists looked for signs of capture myopathy (e.g., coffee-colored urine, white striations in muscle), but diagnosis is difficult, especially for extremely young animals (A. Wuenschmann, University of Minnesota VDL, personal communication).

When I found a GPS collar without a carcass or other evidence of predation, I backtracked to the last known locations of the calf and its dam to conduct an expanded search. The Iridium adult collars were more accurate than the Globalstar calf collars, so I used the dam's location from the approximate time of death of the calf to search for evidence of a mortality. Once the calf collar was located, I determined the collar to be slipped rather than associated with mortality when the breakaway section was frayed or the bolts holding the breakaway section were loose, coupled with both an absence of blood on the collar and lack of mortality evidence within a 30-m radius of the collar. Also, dams rarely fled the site of a slipped collar, whereas they typically fled when a calf was preyed upon.

RESULTS

Monitoring for Calving

I observed 48 of 73 (66%) monitored cows localize during May–June. Of these 48, 47 (43 pregnant, 4 unknown pregnancy status) made a long-distance calving movement followed by localization (Fig. 2); the cow that did not make a long-distance movement was pregnant. In total, 44 of 50 (88%) pregnant cows localized. Four non-pregnant cows

localized during this time. Mean path length from start of the calving movement to localization was 5.4 km (± 0.7, 0.4–22.7 km) and mean displacement was 2.1 km (± 0.3, 0.05–13.4 km). These movements occurred over 14.4 hours (± 1.5, 1.0–42.5 hr). Calving occurred during 2 May–2 June 2013. Mean and median calving date for all monitored females was 14 May (± 0.9 days); 73% (35 of 48) of the calving localizations occurred 6–17 May. Overall, monitored cows (pregnant and unknown pregnancy status) presumed to have calved localized for 3.3 days (± 0.3, 1.1–14.7 days) at calving sites, but cows whose calves were collared localized less than half as long at calving sites as cows whose calves were not collared (Table 1). Of the 48 cows that localized, 32 (67%) moved 415 m (± 66.9, 42.5–1,821 m) to a secondary post-parturition site before again localizing for 4.2 days (± 0.5, 0.6–12.2 days). Cows that were approached to collar calves moved farther and remained at their secondary site longer, than cows that were not approached (Table 1). Of 32 cows that moved to secondary localization sites, 22 had their calves captured. All cow-calf groups spent 6.1 days (± 0.5, 1.1–14.7, n = 48) in post-parturition areas (birth site plus subsequent localization). I observed no effect of capture on duration localized in post-parturition areas (Table 1).

The automated reports accurately flagged 14 dams as localized; subsequently 24 of their calves were collared. The reports flagged 1 dead moose, and 3 moose that localized after their calves were collared (i.e., 4 false positives). The reports did not flag 17 dams that were approached (based on our on-screen observations of their movements) for neonate capture, and 12 dams that appeared to have made movements indicative of calving (3 within the capture operation window), but were not approached (i.e., 29 false

negatives). I do not know if 2 cows were flagged since reports were not generated for 2 days due to technical problems.

Calf Capture and Handling

I collared 49 calves of 31 dams during 8–17 May 2013. Mean bonding time (duration of localization before capture minus 12 hr) was 40.2 hours (± 3.7, 21.9–132.4 hr, n = 31). Of the 31 dams, 28 were confirmed pregnant by serum progesterone during the previous winter, and 3 were unknown. In total, 39 cows were approached for neonate capture; 31 of these were observed with ≥1 calf. Of the 8 cows not observed with a calf, 1 cow was dead, 4 were pregnant, and 3 were not pregnant. Two of these cows (1 confirmed pregnant, 1 not pregnant) were revisited 1–2× with no calf spotted. The monitoring (using automated flagging combined with examination of movement plots by eye) therefore accurately predicted calving for 31 of 38 live cows (82%). Assuming the 4 pregnant cows calved, but I could not find their calves, our success rate was 35 of 38 live cows (92%). We approached 11 cows (8 pregnant, 3 not pregnant) that had exhibited movement patterns indicative of calving, yet no calf was observed at first approach. I revisited 6 of these cows (5 pregnant, 1 not pregnant) 1−3×, because they were behaving as if a calf was nearby (e.g., reluctant to move away from the local area where observed, looking back at the area) or each cow remained localized following the first approach by the crew. During a subsequent observation the helicopter crew captured ≥1 calf with 4 of these 6 cows, all known to be pregnant. Five cows (3 pregnant, 2 not pregnant) were approached once with no calf observed and not revisited.

I captured 18 sets of twins and 13 singletons (58% twinning rate) throughout the capture operation; 7 of the singletons were captured in the last 2 days of the operation.

Twins accounted for 71.4% of calves captured during the first 8 days, but only 30% during the final 2 days of the 10-day operation. Median calving date of our study cohort dams (the 31 whose calf(ves) were handled) was 12 May 2013 (range = 5–16 May) and the mean date was 11 May 2013 (± 0.6 days). In an effort to reduce handling time, the crew measured all morphometrics for only an initial subset of calves (n = 11). Overall, handling times averaged 9.1 minutes (± 2.27, 3–18 min, n = 16). Handling times averaged 12.3 minutes (± 0.3, 7–18 min, n = 10) for captures timed by the spotter plane (8–12 May), with singletons taking less time than twins (9.0 versus 14.5 min). Handling times were reduced to 3.7 minutes later during 13–14 May (± 1.2, 3–5 min, n = 6, all twins) when handling times were recorded by the capture crew and handling protocols were shortened in an attempt to mitigate capture-related abandonment (DelGiudice et al. 2015).

Calf Collars

Of 38 mortalities investigated on site, 11 of the collars failed to send a mortality alert text message. Three of these collars were buried, which blocked transmission of its mortality message to the satellite base station (and stopped sending GPS fixes); 1 was on a drowned calf in flowing water (causing collar motion); 5 sent mortality transmissions to the base station, but the base station did not send an email or text alert; and 2 simply did not send a mortality transmission to the base station. It is unknown whether the collars that never sent a mortality transmission to the base station were in VHF mortality mode, because this was not checked in the field in these instances.

On 26 November 2013, I investigated a calf mortality (systemic infection resulting from wolf-inflicted wounds). The expandable collar had caused abrasions on

the dorsal aspect of the neck. On 17 January 2014, a collar dropped as designed, but prematurely. The band had expanded and there was no evidence of neck abrasion. One calf collar stopped transmitting GPS coordinates on 13 August 2013 (VHF was still functional). I captured this calf on 6 February 2014 to remove its collar and observed an expandable band-caused abrasion on the top of its neck. Consequently, I captured and removed all remaining collars (7–10 February 2014, $n = 7$). Neck abrasions were evident on 7 of 9 calves aged ~6.5–9 months old. The prognosis was good for the calves that exhibited abrasions in our study (T. J. Kreeger, University of Minnesota, personal communication).

Collars weighed 420 g, which was 2.6% of mean total body mass at capture (16.0 ± 0.3 kg, $n = 43$; Severud et al. 2014). Moose calves exhibit a self-accelerating growth phase during which they gain 1.3–1.6% body mass/day for the first 150–165 days of life (Schwartz and Renecker 2007); however, I recovered 1.6- and 6.7-month old carcasses that weighed 46.7 kg (with missing head and gastrointestinal tract) and 136.4 kg (intact but emaciated; W. J. Severud, unpublished data), representing a 0.9% and 2.4%/day growth rate, respectively. At a conservative rate of 0.9%/day growth, our collars would be <1% of mean body mass by 110 days, but at our observed 2.4%/day this would be at 43 days. In each case, collar mass was well below the 5–10% of body mass recommended by the American Society of Mammalogists (Sikes et al. 2011).

Mortality Investigations

Mean time elapsed between estimated death (backtracked 6 hr from when collar entered mortality mode) and mortality investigation (response time) was 53.3 hours (± 15.3, 0.3–579 hr, $n = 38$). This included slower response times due to extraordinary circumstances.

One slipped collar was inaccessible for 24 days (located on an island with the surviving collared twin and dam); 1 collar was buried, unable to transmit, and failed to send text alerts; and 3 were associated with project staff taking mandatory time off due to human safety concerns. With these outliers and the capture-related mortalities excluded, the mean response time was 27.5 hours (± 2.9, 9.4–74 hr, n = 22). Response times were slower ($t_{17} = -2.10$, $P = 0.03$) when I investigated multiple mortality sites/day compared to a single site ($\bar{x}_{\text{multiple}} = 54.25 \pm 0.5$, 0.3–192 hr, n = 16 versus $\bar{x}_{\text{single}} = 27.5 \pm 0.1$, 9.4–49 hr, n = 21). Mean distance from a collar's transmitted location when it entered mortality mode to the mortality site was 91 m (± 24.2, 4–502 m, n = 33). Mean distance from the UTM coordinates used for navigation (most recent location) to the mortality site was 69 m (± 15.2, 3.6–401 m, n = 34).

As of 31 December 2013, I documented 36 mortalities and 4 slipped collars; 9 collared calves remained "on air." Capture-related activities accounted for 11 of the mortalities, including 9 following abandonments, 1 accidental (stepped on by the dam), and 1 unknown cause (DelGiudice et al. 2013). Three of the 4 slipped collars came off when calves were 13–15 days old, and 1 at 31 days old. Of the remaining 25 natural mortalities, there was 1 death following natural abandonment (dam and calf were together after capture for 80 hr before abandonment), 1 following abandonment of unknown cause (together after capture for 17 hr), 1 drowning, 1 unknown predator-kill, 1 lethal infection from a wolf bite, 4 bear-kills, 12 wolf-kills, and 4 "probable wolf-kills." Histological and disease-screening results from the VDL revealed no contributing factors associated with the natural mortalities. After censoring capture-related mortalities and

slipped collars, 25 of 34 calves (74%) died as of 31 December 2013, with 21 (84%) due to predation. About 50% of collared calves died before 50 days of age.

Dams fled from calf predation events (first location post-estimated time of death) 21× farther ($\bar{x}$ = 623 ± 90, 28–1,517 m, n = 22) than from slipped collars ($\bar{x}$ = 29 ± 15.1, 1–76 m, n = 4). A dam fled 2,476 m from the single drowned calf.

I retrieved 14 intact carcasses and 1 partial carcass (missing left kidney, gastrointestinal tract, part of liver) and delivered them to the VDL for necropsy. Of these, causes of death included hypoglycemia due to capture-related abandonment (n = 9), capture-related mortality (1 unknown cause, 1 fractured skull resulting from trampling by dam), emaciation and infection likely resulting from wolf-bite (1), drowning (1), hypoglycemia due to abandonment of unknown cause (1), and bear predation (1). Hypoglycemic calves had no curdled milk in their abomasum, but often varying amounts of vegetation in their rumen, indicative of abandonment by their dams. Thirteen of the retrieved carcasses were of neonates (3–12 days old) and 2 were of calves 1.6 and 6.7 months old (bear-kill and infection, respectively). Carcasses of wolf-killed calves were never retrieved because wolves typically consumed the entire carcass quickly or moved the collar enough to keep it in active mode and delay our investigation. I also retrieved an incidental (uncollared) intact carcass that died of infection likely due to a wolf-inflicted wound (3 months old).

DISCUSSION

Monitoring for Calving

My monitoring method has served as the first large scale attempt to monitor moose calving accurately without the use of more invasive methods (e.g., vaginal implant

transmitters [VITs]). During a recent moose calf mortality study in 2 locations in Ontario, Canada, 64 VITs were deployed in 1 study area and 67% of those VITs resulted in a successful assessment of calving, while 58% resulted in successful capture of neonates (difference due to calves that were stillborn or too mobile for capture). In the other study area 35 VITs were deployed but resulted in only 1 successful capture. Calves in that area were not able to be captured from "most" cows fit with VITs due to either maternal aggression or remote calving location (Patterson et al. 2013: 3), but it was not reported how many of these 35 cows were observed with a calf. VITs were also deemed costly and logistically difficult (Patterson et al. 2013). Thus, my approach provides a potentially significant improvement over the use of VITs.

Fitting GPS collars facilitated intense monitoring of both cows and calves to meet several study objectives in a cost- and labor-effective manner. Localizations, detected by computer-monitoring of cows, were a clear indication of calving, even though the automated cow movement reports did not always flag cows as "localized." Consequently, I often identified localized cow patterns visually on the screen rather than by relying on the "localization flag" (i.e., moved <100 m in 36 hr after a long distance move). Other studies have used movement patterns of ungulates to infer calving with varying success (Welch et al. 2000, Vore and Schmidt 2001, DeMars et al. 2013, Asher et al. 2014, McGraw et al. 2014).

In my study, almost all of the cows made a long distance calving movement prior to their localization, which is higher than in previous studies (NE Minnesota: 88%, McGraw et al. 2014; Alaska: 20%, Bowyer et al. 1999). However, the mean displacement and path length that we observed were similar to those reported by McGraw

et al. (2014; 3 and 6 km, respectively). In Alaska, 20% of pre-parturient cows made an average 7.3-km movement immediately before calving, but that study used VHF collars so shorter calving moves may have been within triangulation error ellipses and therefore masked (Bowyer et al. 1999). In another Alaskan study, cow daily movements greatly increased 2 days prior to parturition, decreased to <120 m/day (close to expected GPS collar error) for 9 days after birth, and did not reach pre-parturition levels until calves were 26 days old (Testa et al. 2000*a*). Mean displacement during the calving movement (4 km) was 2× the mean distance I observed.

In my study, about two-thirds of the dams moved to a secondary post-parturition site, which was similar to that found by McGraw et al. (2014). Overall, the limited distance of dam movements may be attributable to the relative immobility and vulnerability of their very young neonates (van Beest et al. 2011), but dams must forage to fulfill heightened nutritional demands of lactation and condition recovery following winter (Verme and Ullrey 1984, Robbins 1993, Schwartz and Renecker 2007).

Calf Capture and Handling

As in my study, an Alaskan study observed twin births more frequently early in the calving period (Bailey and Bangs 1980). From 2004–2010, mean estimated twinning rate in northeastern Minnesota was 29% (± 2.6, 18–39%; M. W. Schrage, unpublished data). In an earlier moose study (2011) in northeastern Minnesota, mean calving date, based on monitoring calving moves of GPS-collared cows and subsequent localizations, was 14 May (range = 3–27 May), with 70% of births occurring during 9–20 May (McGraw et al. 2014). Calves were not approached or captured in that study. My study cohort's mean

calving date was earlier (captures restricted to 8–17 May), but was similar for all adult cows monitored for calving in 2013.

Calf Collars

In my study, even though the collar was within acceptable weight ranges, the expandable band caused abrasions on the top of the neck of several calves. Lesions have been reported from ill-fitting collars on mule deer (*O. hemionus*) and bighorn sheep (*Ovis canadensis*), but all healed well (Krausman et al. 2004). My band was likely too narrow for the total weight of the GPS collar. I described this problem to the manufacturer and the band was redesigned for future studies.

Circumstances influencing proper collar and modem function precluded timely mortality notifications and investigations in several instances. When I did not receive mortality alert text notifications or did not investigate due to personnel safety issues, mean response time basically doubled. Response times were close to daily monitoring of VHF collars (Barber-Meyer et al. 2008, Patterson et al. 2013), but only if daily flights are possible given fair weather and working equipment. Some collars did not send a text message after a mortality; consequently, I began to also closely monitor the status of cow-calf(ves) collars using the GPS Plus X software and proximities using the Vectronic website to determine possible mortalities. Working with the vendor it was determined that our modem power was not strong enough, potentially inhibiting transmission of mortality text notifications. An antenna booster greatly improved cellular signal strength, and since then we have not documented further problems. Additionally, the Globalstar satellite system is not as comprehensive as the Iridium system (Tomkiewicz et al. 2010), and therefore is not as reliable. Bears caching collars or calves drowning and remaining

in flowing water may either keep a collar from transmitting or keep it in normal mode due to motion. Similarly, predators or scavengers may "play" with the collar and keep it in normal mode long after mortality has occurred. In some cases, predators moving collars likely also accounted for long distances between where we located a collar and where the mortality event occurred, but in most cases, collars were recovered in close proximity to mortality sites. Exceptions included a bear caching a head (with the collar) 400 m from the mortality site, and wolves moving a collar 500 m around the shore of a permanent wetland. These noteworthy field observations will be of value in how I monitor calves and their dams from the beginning of future capture operations. Arriving at mortality sites in a timely manner allowed retrieval of entire carcasses and afforded more certainty when assigning mortality cause.

Mortality Investigations

My observed natural mortality rate was similar to estimates in northeastern Minnesota (60%; Lenarz et al. 2010), but much higher than a recent study in Ontario (36%; Patterson et al. 2013). In my study, about half of the collared calves died before 50 days of age, consistent with studies of moose and other ungulate neonates demonstrating the highest hazard in the first months of life where predators are present (Ballard et al. 1991, Testa et al. 2000*a*, Carstensen et al. 2009, Patterson et al. 2013).

Just as fitting GPS collars to dams proved highly valuable in allowing us to locate parturition sites, capture and GPS-collar neonates, subsequently monitor movements of both, and respond rapidly to investigate mortalities, this technology and associated monitoring tools should prove to be of significant value in closely examining other aspects of ungulate ecology and management. Species inhabiting heavily forested

landscapes or that are otherwise cryptic during calving could be monitored in this manner, and population demographics such as calving rate and neonatal survival can be more accurately assessed by reducing bias in analyses. Intensive monitoring made possible by GPS collars offers a greater quantity and higher quality of data from which to synthesize valuable information and enhance our understanding of ecological relations critical to management. This can be done in an unprecedented, comprehensive, and efficient manner.

Table 1. Time spent (days) at and distance traveled (m) between primary and secondary post-parturition sites by female moose, May–June 2013, northeastern Minnesota.

	Approached to collar calves					Not approached							
	$\bar{x}$	SE	min	max	*n*	$\bar{x}$	SE	min	max	*n*	*t*	df	*P*
Duration at primary site (days)	2.4	0.2	1.4	6.5	31	5.1	0.7	1.1	14.7	17	3.5	19	≤0.01
Distance moved to secondary site (m)	504	88.2	62.0	1,821	22	220	56.1	42.5	654	10	−2.7	30	0.01
Duration at secondary site (days)	4.8	0.6	0.9	12.2	22	2.9	0.5	0.6	5.3	10	−2.3	28	0.03
Total localization (days)	5.8	0.6	1.5	14.0	31	6.8	0.9	1.1	14.7	17	0.9	32	0.35

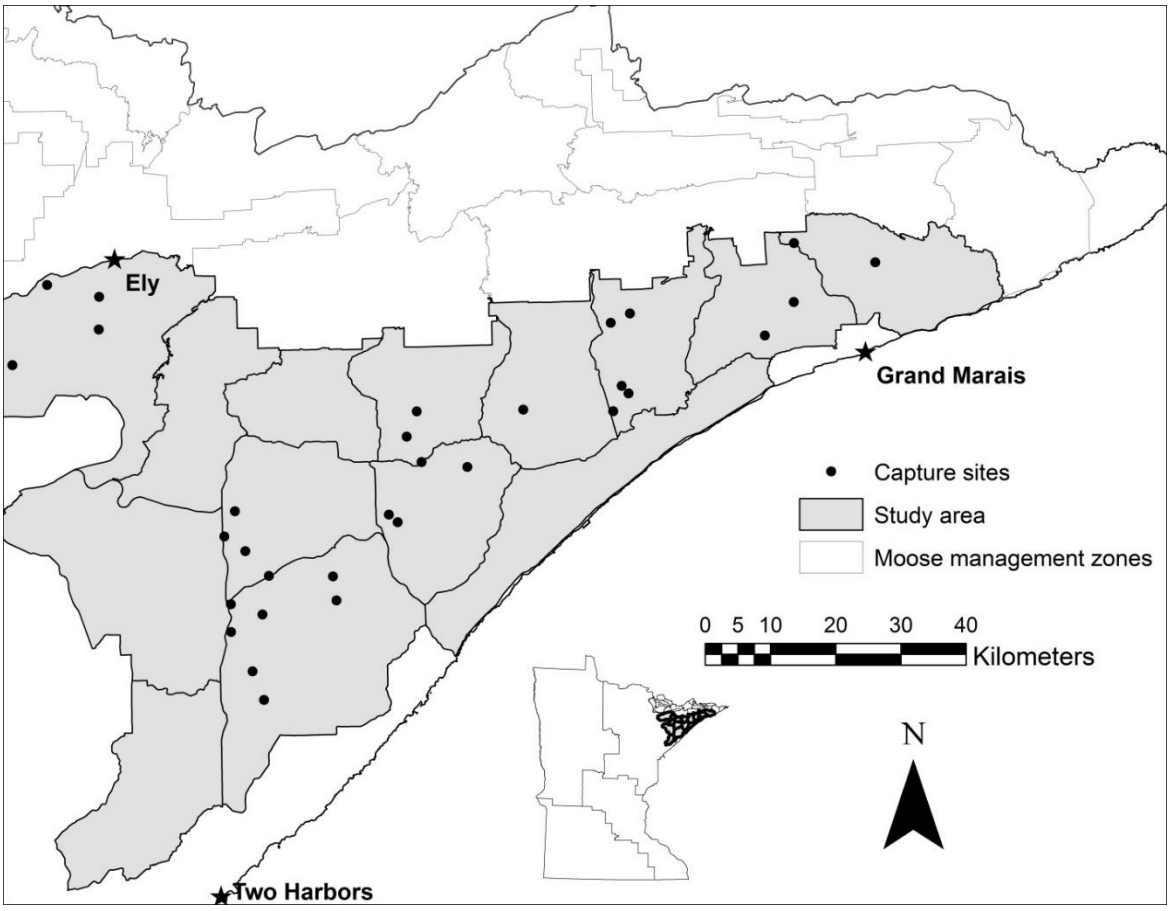

Figure 1. Capture sites (n = 31) of moose neonates (6,636 km^2-study area), 8–17 May 2013, northeastern Minnesota.

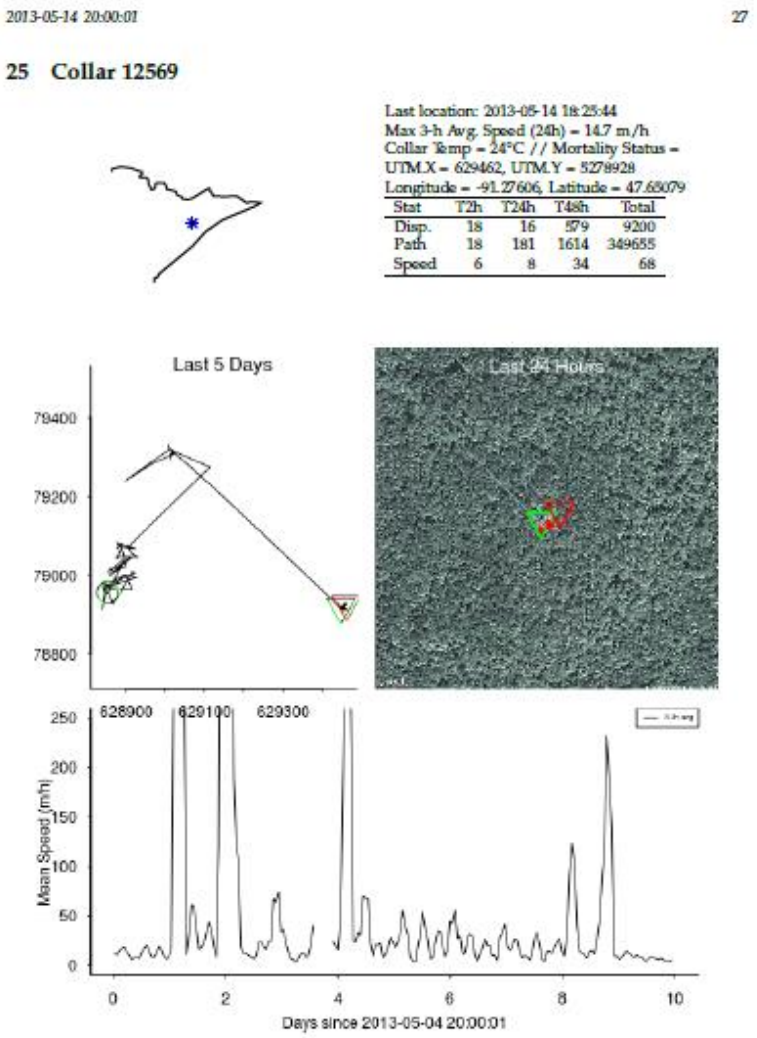

Figure 2. Example report for adult female moose number 12569 from 20:00 hours, 14 May 2013, northeastern Minnesota, showing movement paths for the past 5 days and 24 hours, and the 3-hour average distances moved per hour (speed). The green circle, green and red triangles represent the start of the 5-day period, the start of the 24-hour period, and the most recent location, respectively. Red dots depict the location when the collar

was “localized.” This cow was approached at 7 days since 4 May (12 May), but she had not yet calved. She made a “calving movement” ~9 days after 4 May 2013 (14 May) and then localized. She was approached on 15 May and her twins were collared.

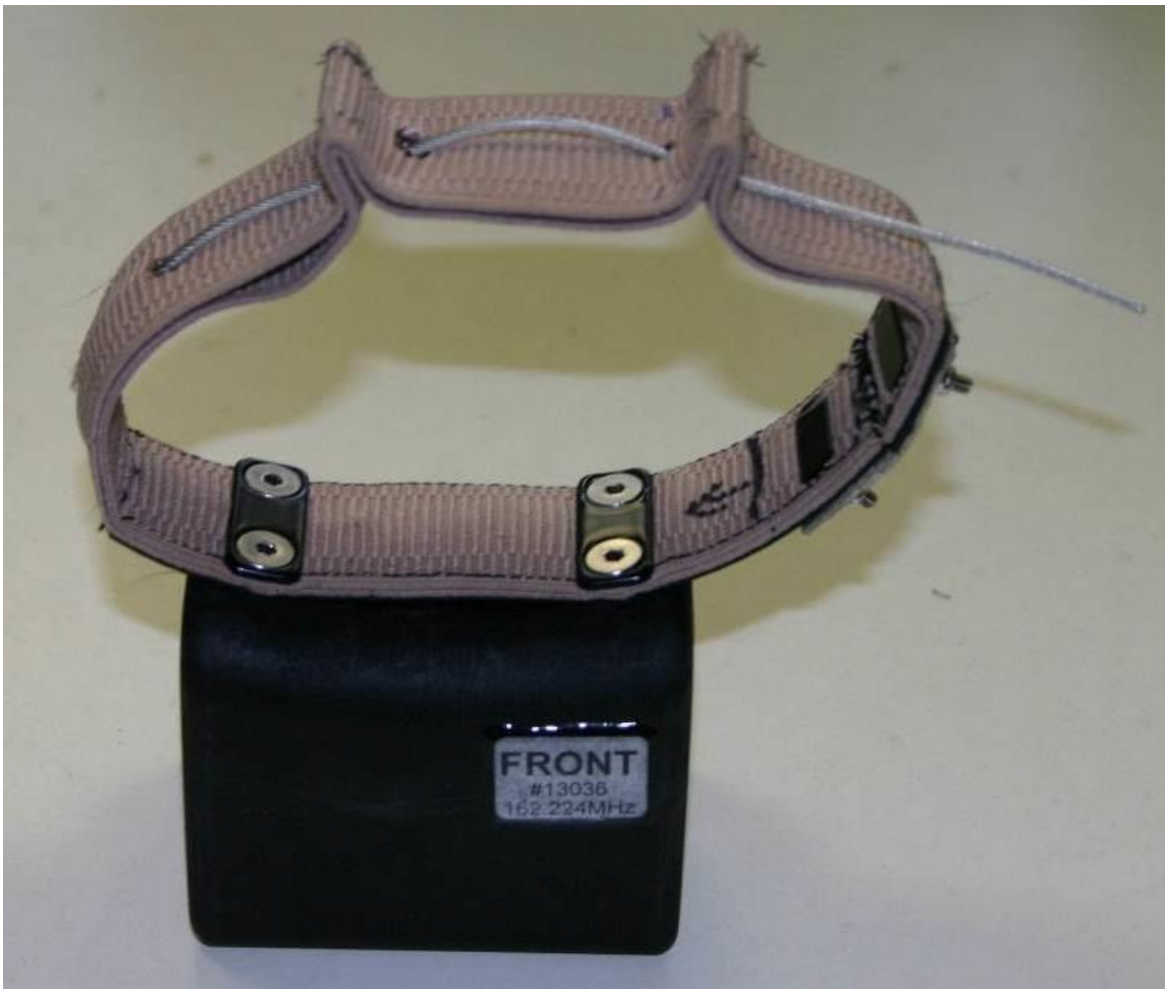

Figure 3. GPS PLUS VERTEX Survey-1 GLOBALSTAR collar with expandable belt (Vectronic Aerospace GmbH, Berlin, Germany) deployed on moose neonates (n = 49), 8–17 May 2013, northeastern Minnesota.

Chapter 2: Survival and Cause-specific Mortality of Calves in Northeastern Minnesota's Declining Moose Population

ABSTRACT Ungulate reproductive success (calf production and survival) is an important driver of population performance. Northeastern Minnesota's moose (*Alces alces*) population has declined 58% from 2006 to 2017. Because causal mechanisms for this decline were largely unknown, I investigated calf production, survival and cause-specific mortality of calves of global positioning system (GPS)-collared dams of this population. In 2013 and 2014, I GPS-collared 54 neonates and monitored them for survival. In 2015, I monitored 50 calving dams for signs of neonatal mortality using behavioral cues, and assessed seasonal calf survival with aerial surveys. In 2013 and 2014 (pooled), collared calf survival to 9 months was 0.34 (95% CI = 0.23–0.52), whereas uncollared calf survival in 2015 was estimated at 0.40 (95% CI = 0.30–0.54). Mortality in all 3 years was high during the first 50 days of life, with hazard peaking at about 15 days of age when dams and calves departed calving sites. In 2013 and 2014 (pooled), calving sites were relatively safe for neonates; predator-kills occurred a mean 31.6 days after departure and 1,553 m from calving sites. Predation was the leading cause of death of collared calves (84% of mortalities), with wolf (*Canis lupus*) predation accounting for 77% of deaths. The cumulative probability of succumbing to all forms of mortality by 9 months of age was 69.8%. Other forms of mortality included drowning, infection, and natural abandonment. I documented higher wolf predation than other recent studies with similar predator communities. Identifying specific causes of calf mortality and understanding their relations to various landscape characteristics and other

extrinsic factors should yield insight into mechanisms contributing to the declining moose population in northeastern Minnesota and serve as a basis for ecologically sound management responses.

INTRODUCTION

Population declines have been attributed to many factors, including poor juvenile survival (Raithel et al. 2007, Pinard et al. 2012, Forrester and Wittmer 2013). Realized population growth of large herbivores is most sensitive to variation in adult survival, but high variability in annual juvenile survival can have a marked impact on population dynamics as well (Gaillard et al. 1998, 2000; Lenarz et al. 2010). When large predators are abundant, predation can be a primary cause of mortality of neonatal ungulates (Linnell et al. 1995, Carstensen et al. 2009, Severud et al. 2015*a*). It is not always clear when predation is compensatory or additive to other sources of mortality (Franzmann et al. 1980, Linnell et al. 1995), although a recent study documented additive seasonal effects of predation on moose (*Alces alces*) calves in Alaska (Keech et al. 2011). Predation's impact on population-wide calf survival rates depends on the extant predator guild and relative densities of predators and prey (Eriksen et al. 2011, Patterson et al. 2013). Less is known about other ultimate and proximate sources of moose calf mortality or contributing factors. The moose population in northeastern Minnesota declined 58% from 2006 to 2017 (DelGiudice 2017). Survival and cause-specific mortality of calves was largely unknown in this area, but using survey flights, average first-year survival from 2002 to 2008 was estimated at 0.40 (range = 0.24–0.56; Lenarz et al. 2010).

Pregnant cow moose tend to move long distances prior to localizing ("calving movement") to give birth (Testa et al. 2000*a*, McGraw et al. 2014, Severud et al. 2015*a*). Localizations at calving sites up to 14 days have been documented (Severud et al. 2015*a*). Dams with global positioning system (GPS) collars also have been observed making repeated movements away from and return-trips to focal areas where calves have been preyed upon (e.g., a "mortality movement;" Severud et al. 2015*b*, Obermoller et al., in press). Expandable GPS collars have until now not been fitted to moose neonates, and have only recently been used on other ungulate neonates (white-tailed deer [*Odocoileus virginianus*], Long et al. 2010; fallow deer [*Dama dama*], Kjellander et al. 2012). Observable fine-scale movement patterns and habitat use of moose calves, made possible by GPS collars, also facilitated rapid investigation of mortality events to assign proximate causes and gather evidence of contributing factors. Having both dams and their calves GPS-collared also allowed me to examine the importance of proximity of dam and offspring to juvenile survival.

My objectives were to estimate survival and cause-specific mortality of GPS-collared moose calves, the first large-scale deployment of GPS collars on free-ranging neonates. I predicted that calf survival would be low (50% and 30% by January and May) and predation would be the leading cause of mortality, with black bears (*Ursus americanus*) having their greatest impact on the youngest calves, whereas wolf predation would occur throughout the year. I also predicted that survival might be influenced by a variety of covariates, including dam age, litter size, calf mass, calf hind foot length (HFL), and proximity between calf and dam.

STUDY AREA

I conducted this study on 6,068 km^2 located between 47°06'N and 47°58'N latitude and 90°04'W and 92°17'W longitude in northeastern Minnesota along the southern extent of moose range in North America (Lenarz et al. 2010). Due to the steady moose decline in this region, State and Tribal harvests were suspended in 2013 until further notice; in 2016 a limited Tribal harvest resumed (DelGiudice 2012). This region has been characterized as the Northern Superior Upland (NSU) within the Laurentian mixed forest province (Minnesota Department of Natural Resources [MNDNR] 2015). The NSU is a mosaic of wetlands, lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*), and upland stands of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white pine (*P. strobus*), and red pine (*P. resinosa*), intermixed with trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Timber harvest declined in the area from 2001 to 2013 (Wilson and Ek 2013).

The most common predators of moose in the area are gray wolves and American black bears, which can have a pronounced effect on calf survival (Lenarz et al. 2009; Patterson et al. 2013; Severud et al. 2015*a*, *b*); wolf and bear densities have been estimated at 4.4/100 km^2 and 23/100 km^2, respectively (Mech et al. in press, Garshelis and Noyce 2011). Primary prey of wolves include white-tailed deer, which are managed at pre-fawning densities of <4 /km^2 in moose range (Nelson and Mech 1981, DelGiudice et al. 2002, MNDNR 2012). Alternate wolf prey included beavers (*Castor canadensis*), and to a lesser extent, snowshoe hares (*Lepus americanus*), black bears, and various small

mammals (Stenlund 1955, Frenzel 1974, Van Ballenberghe et al. 1975, Chenaux-Ibrahim 2015).

METHODS

Adult Moose Capture and Handling

In January and February 2013–2015, 129 adult female moose were captured, handled, and fitted with GPS collars as part of the MNDNR's study of cause-specific mortality (Butler et al. 2013; Carstensen et al. 2014, 2015). An incisor was pulled to estimate age and the moose was blood-sampled to test for pregnancy. Capture and handling protocols met American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). Adult collars collected locations every 4 hours for the majority of the year, but were reprogrammed to an hourly schedule during and immediately following calving (May and June).

Calf Capture and Handling

I monitored collared adult females for a calving movement (an atypical long distance movement followed by intense localization) and subsequently located calves by approaching clusters of location-fixes (Severud et al. 2015*a*). In 2013, a capture crew (Quicksilver Air, Inc., Fairbanks, AK) located eligible calves (>24 hr old) via helicopter and then landed to allow 1–2 handlers to disembark. In 2014, in response to a high level of capture-induced abandonment during 2013 (DelGiudice et al. 2015), all captures were conducted without the assistance of a helicopter. Typically, handlers were able to easily approach and capture calves. Immobilizing drugs were never used on the dams or calves during calf captures. Each calf was weighed (±0.5 kg) by spring-scale, ear-tagged, and

blood-sampled. Morphological measurements (hind foot length [HFL], upper and lower neck circumference, chest girth, total body length [±1 cm]) and rectal temperature (±0.05° C) were recorded, and GPS collars fitted (see details below). I estimated age of calves based on localization of the dam (birth was assumed to occur ≤12 hr of initial localization). Twins were handled, collared, and released together to minimize the risk of capture-related abandonment (Keech et al. 2011, DelGiudice et al. 2015). I placed collars in bags with vegetation and other ground debris for ≥24 hours before captures to minimize human and collar scent. In 2014, I also placed clothing and other capture-related gear in similar bags. All calf captures and handling protocols followed requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (Protocol 1302-30328A) and were consistent with guidelines recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

In response to capture-induced abandonment of calves and capture-related mortality of adults (DelGiudice et al. 2014, 2015; Carstensen et al. 2015), the Governor of Minnesota issued Executive Order 15-10 (28 Apr 2015), barring state agencies from conducting or permitting any collaring of moose in the state. For the 2015 calving season, I monitored existing GPS-collared adult females for a calving movement, and tracked dam behavior for indications of a "mortality movement" (see below).

Calf Collars

In 2013, calves were fitted with a GPS PLUS VERTEX Survey-1 GLOBALSTAR collar with an expandable belt (420 g, box dimensions 85 × 59 × 75 mm, belt 3 cm wide, initial

circumference 35 cm, fully expanded circumference 65 cm; Vectronic Aerospace GmbH, Berlin, Germany). For additional details on collars, see Severud et al. (2015*a*). Summer field tests demonstrated that mean linear error (±SE, range) of calf collar locations was 24.9 m (±2.7, 1–274 m) under open canopy and 40.3 m (±1.3, 0–368 m) under dense canopy of forested cover types (≥80% closure; Obermoller et al. in review). In 2014, collar bands were modified in response to neck abrasions (Severud et al. 2015*a*) to include a new polyester and elasthodiene band increased to 5.0 cm width, an increased number of expansion loops (4), and a clear plastic tubing over the dorsal aspect of the band. This modified collar weighed 515 g (3.2% of body mass), but was reduced to 455 g (2.8% of body mass) when I removed the plastic tubing after deeming it too visually conspicuous (Obermoller et al. in press). All collars were below the 5–10% of body mass recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016), and because calves grow rapidly early in life (Schwartz 2007), collar weights were <1% of body mass within about 40 days (Severud et al. 2015*a*).

Dam-calf Monitoring

In 2013 and 2014, I monitored collared dam-calf groups several times daily as updated locations were received by the base station. I examined proximity and synchrony of dam-calf GPS locations until fate was known (mortality, slipped collar, failed collar). When I received a mortality alert text message or suspected (via monitoring) a mortality had occurred, a response team initiated an investigation to determine cause of death. See Severud et al. (2015*a*) for details of mortality investigations. In response to a high rate of

slipped calf collars in 2014, I assessed their apparent survival via helicopter in March 2015 by locating their GPS-collared dams.

In 2015, I used calving movements to indicate calving activity, and then "mortality movements" to trigger mortality investigations of calves using flee and return patterns of the dams (Severud et al. 2015*b*, Obermoller et al. 2017). I estimated time of death using the time at which the dam initially fled. I conducted flight surveys via helicopter to assess apparent seasonal survival rates in 2015 during late November–early December (~190 days old) and late March 2016 (~320 days old). If a calf was not observed with a dam, I estimated date of death as the midpoint between its last known date alive and the flight. In 1 case, a dam's collar was not transmitting during calving, but began functioning again before flights; I imputed the median 2015 calving date for this individual.

Survival Analysis

I calculated Kaplan-Meier survival estimates, smoothed hazards, and fit Cox proportional hazard models using the R packages *KMsurv*, *muhaz*, and *survival*, respectively (R Core Team 2017). Since calf births were tightly synchronized (Severud et al. 2015*b*), I calculated survival by calf age, with day 0 being birth (Fieberg and DelGiudice 2009). For smoothed empirical hazard curves, I used a k-nearest neighbors distance bandwidth. I calculated cause-specific mortality rates with a cumulative incidence function using the R package *wild1* (Sargeant 2011). Dam and calf location data were screened for locations that were thought to be erroneous fixes (V. St-Louis, MNDNR, unpublished data). I then calculated proximity between cows and their calves. I estimated birth-dates

of all calves (2013–2015) based on dams' calving movements (assumed calved ≤12 hr after the cow localized). To test if calf survival was affected by dam-abandonment behavior, I used a log-rank test in the function *survdiff* from the R base package *survival* to compare survival curves of non-abandoned twins whose twin was abandoned to calves of non-abandoning dams (Harrington and Fleming 1982, Therneau 2015). I tested for independence of twins using Kruskal-Wallis rank sum test (Testa et al. 2000*b*). In 2013 and 2014, time of death was estimated using the mortality mode of collars, and calf and dam locations relative to the mortality site. In 2015, time of death of uncollared calves was calculated as initial flee from a focal point where I located calf remains. Missing data (dam age, HFL, mass) were imputed 20 times using the function *aregImpute* in the R package *Hmisc*. I then ran a correlation matrix on the numerical covariates and eliminated correlated variables ($|r| > 0.6$). I used analyses of variance (ANOVA) to examine correlation among categorical variables, excluding highly correlated covariates. I stratified models by calf age (in days; neonatal: 0–50, more mobile calf: >50). Stratifying by covariate allowed covariate effects to vary across strata. I then employed Cox proportional hazards models with the resulting reduced set of variables with each imputed data set. Coefficients were averaged over the 20 imputations. I additionally applied a separate Cox model using daily survival with mean daily proximity between calf and dam as a covariate. All models were tested for the assumption of proportionality using the function *cox.zph* in the *survival* R base package. Means ± standard error and range are reported throughout unless otherwise noted.

RESULTS

I collared 49 calves from 31 dams in 2013 and 25 calves from 19 dams in 2014 (58% and 32% twinning rates, respectively). Overall, the sex ratio of collared calves was 36 females: 38 males, which was not different from parity (binomial test, $P = 0.49$). Seven dams abandoned 9 calves in 2013 and 6 dams abandoned 9 calves in 2014 (DelGiudice et al. 2014, 2015). Two additional calves died during or shortly after capture from trampling by the dam and not nursing due to unknown causes (DelGiudice and Severud 2016). These 20 calf fates were associated with capture and therefore not included in survival analyses. Of the remaining 54 calves, 4 slipped their collars in 2013 and 10 in 2014; 40 calves remained for study of survival and natural cause-specific mortality. In 2015, I observed calving movements or localization of 50 GPS-collared cows and tracked those dams for mortality movements. Assuming a 30% twinning rate (M. Schrage, Fond du Lac Natural Resource Management Division, unpublished data), this yielded an estimated 65 uncollared calves for monitoring during 2015. Median calving dates for 2013, 2014, and 2015 were 14, 19, and 10 May, respectively.

Survival distributions of calves of dams that abandoned one calf from a set of twins did not differ from calves of non-abandoning dams, so all collared calves were retained in analyses ($\chi^2_1 = 0.10$, $P = 0.72$). Survival distributions of twins that died together versus those that died separately did not differ, so I analyzed all calf fates as independent ($\chi^2_1 = 0.40$, $P = 0.53$).

Blood profiles of calves sampled in 2013 were reported elsewhere (DelGiudice and Severud 2016). Mean rectal temperature was 38.7 °C (± 0.07, 37.7–39.7 $n = 43$).

For all collared calves, mean total body mass at capture was 15.8 kg (± 0.3, 12–20.5, n = 38) and mean HFL was 45.9 cm (± 0.3, 42–49, n = 42). Body mass and HFL were correlated (r = 0.64, P <0.001). There were no significant differences in mass or HFL by sex or between twins versus singletons. I reduced the set of independent variables for Cox models using correlation analyses to birth-date, HFL, and litter size, eliminating dam age, calf mass, and calf sex. Mean dam age of all collared calves was 6.4 years old (± 0.5, 1–14, n = 43) and did not differ by calf survival. Median monthly proximity between dam and calf was 67.4 m (±10.3, 34.4–1,593.5, n = 161), with a trend of calves and cows moving farther apart as summer progressed and then coming together through winter (Fig. 2). One calf was excluded from proximity calculations, because it separated from its dam and twin in November by >28 km. It survived alone from November until February when it was recaptured and its collar removed. Dam age, HFL, and birth-date did not meet assumptions of proportionality for Cox models based on Schoenfled individual tests (mean global P = 0.03) and diagnostic plots, nor did mean daily proximity (global P <0.001). Including time as a stratum did not improve model fit.

For pooled 2013 and 2014 collared calves, 30-day survival was 0.58 (95% CI = 0.46–0.74, Fig. 3) and declined to 0.34 (95% CI = 0.23–0.52) by 206 days of age (6–10 February 2014), when all remaining collars were removed (Fig. 3). Follow-up flights assessed survival of calves that slipped their collars, which adjusted survival to 0.29 (95% CI = 0.18–0.46) by 206 days of age. Nearly 80% of mortalities occurred by 1 July (~50 days old) and 95% by mid-August (~100 days old).

In 2015, I observed calf mortalities during the first 30 days of life, as indicated by mortality movements of dams. Based on confirmed calf mortalities (remains located), 30-day survival was 0.85 (95% CI = 0.76–0.94). I suspected additional calves died based on mortality movements, but was unable to locate calf remains. Based on suspected *and* confirmed calf mortalities (mortality movement of dam or remains located), 30-day survival was 0.68 (95% CI = 0.57–0.80). In all 3 years, survival dropped dramatically from birth to age 50 days. Helicopter flights in early winter (30 Nov–3 Dec 2015) and late winter (28–29 Mar 2016) indicated survival of 0.43 (95% CI = 0.33–0.57) and 0.40 (95% CI = 0.30–0.54), respectively.

For collared calves in 2013 and 2014, the empirical hazard function was low initially, then peaked at about 15 days old before declining, followed by a second spike at about 90 days of age (Fig. 4). Mean age of death of calves that died of natural causes before 1 year of age was 35 days old (± 7, 3–205, n = 31), but the median age was 18.3 days, near the peak in hazard. In 2013 and 2014, mortalities from predation (n = 26) occurred a mean 31.6 days (± 6.5, median = 17, range = 0–120.5) after departing from the calving site and occurred 1,553 m (± 289, median = 1,142, range = 107–5,788) from the calving site.

I documented 31 natural mortalities of collared calves in 2013 and 2014. Mean response time from estimated time of death to site investigation was 24.9 hours (±2.3, range 9.5–52.5, n = 23) when collars were working properly. Specific causes of mortality included 20 wolf-kills, 5 bear-kills, 2 natural abandonments, and 1 each of the following: drowning, abandonment of unknown cause, unknown predation, and septicemia resulting

from wolf-inflicted wounds. Cumulative incidence functions of mortality rose rapidly from birth to 50 days of age (Fig. 5). Over the first 9 months of age, the cumulative probability of being preyed upon by wolves or bears was 50.2% (90% CI = 37.1–63.5) and 11.7% (90% CI = 3.5–19.9), respectively, or of succumbing to other causes was 9.6% (90% CI = 2.9–16.3). Predation accounted for 84% of all natural mortalities, with wolves having the greatest impact overall (77% of predation events). I documented 11 natural mortalities (9 wolf-kills, 1 bear-kill, and 1 unknown predator-kill) of uncollared calves born in 2015; no non-predation mortality was observed.

DISCUSSION

As predicted, I observed low annual survival for calves. However, survival dropped to 50% much earlier than predicted (by July rather than January). I was unable to monitor survival to 1 year of age (i.e., recruitment) due to collar removal and slippage (Obermoller et al. 2017), but 9-month survival estimates aligned closely with my annual survival prediction (30% vs observed 28.5%). Mortalities dropped dramatically and stabilized after 100 days of age, similar to other moose calf survival studies with predator guilds that included wolves and bears (Ballard et al. 1981, Hauge and Keith 1981, Larsen et al. 1989, Patterson et al. 2013). These findings are in stark contrast to recent findings in wolf-free New England, USA, where calf mortality was concentrated in late winter-early spring due to a combination of winter tick (*Dermacentor albipictus*) infestation, lungworm (*Dictyocaulus viviparus*) parasitism, and poor physical condition (Musante et al. 2010), and 60-day survival was estimated at 77–94% (compared to my 47%; Jones et al. 2017).

Estimated 2015 annual survival was 17% higher than pooled survival of collared calves in 2013 and 2014 (yet within 95% confidence intervals). These levels closely match rates estimated in this study area by Lenarz et al. (2010) during 2002–2008, before the declining trend was indicated by the MNDNR annual survey (DelGiudice 2017). My observed rates approach those reported in northern New Hampshire, northeastern Alberta, and western Interior Alaska (0.29–0.45; Hauge and Keith 1981, Musante et al. 2010, Keech et al. 2011), but are 46% lower than rates observed in Ontario (0.64; Patterson et al. 2013). Low juvenile survival can be an early indication of reduced resources, followed by increased age at first reproduction, reduction in reproductive rates, and ultimately an increase in the adult mortality rate (Eberhardt 2002). Moose in northeastern Minnesota have been exhibiting signs of each of these recently (Lenarz et al. 2010, Carstensen et al. 2017).

As predicted, predation was the primary cause of neonate mortality, consistent with findings of other moose calf mortality studies conducted in areas with extant predators (Ballard et al. 1981, Hauge and Keith 1981, Keech et al. 2011, Patterson et al. 2013). Contrary to my prediction, bear predation was relatively low, but impacted younger calves, as I predicted (occurred on calves aged 10–48 days). Franzmann et al. (1980) also found that bear predation occurred when moose calves were small and nearly ceased when calves were 1–2 months old, after which time calves were mobile enough to evade bears. A concurrent investigation conducted adjacent to my study area observed equal amounts of bear and wolf predation on moose calves (T. Wolf and S. Moore, Grand Portage Band, personal communication). This area is assumed to have similar bear

densities as my study area, but there may be jurisdictional differences in bear management. Since harvest can influence age and sex structure of bear populations, and adult male bears are more likely to kill large prey, moose calves may experience lower bear-kill rates in areas with fewer adult male bears (Patterson et al. 2013). A study in Ontario, Canada with a similar predator guild also found equal bear and wolf predation, but bear densities were higher than ours (31–45 vs 23 bears/100 km^2; Patterson et al. 2013). The authors postulated that bear sex and age structure may have influenced predation rates more than simple abundance. Indeed, (Ballard 1992) concluded that bear or moose density has little effect on predation rates.

Wolf predation on calves decreased at about 100 days of age, whereas I predicted wolf-kills would occur year-round. Historically, wolves and moose have been sympatric in this system, yet wolves have recently been implicated in the moose population decline (Mech and Fieberg 2014, Severud et al. 2014, Carstensen et al. 2017). In a portion of moose range in northeastern Minnesota, an increasing wolf population was subsidized by deer while also preying upon moose calves which contributed to a moose decline (Barber-Meyer and Mech 2016). Also, unhealthy moose were more vulnerable to wolf predation throughout northeastern Minnesota (Mech and Nelson 2013, Carstensen et al. 2017). Statewide wolf population estimates remained stable during 2012–2016 (Erb et al. 2016). A concurrent wolf diet study in northeastern Minnesota found high occurrence of calves in spring diets (11 May–30 June), and although calves did not represent a majority of wolf diet by biomass, a relatively high number of calves were likely consumed

(Chenaux-Ibrahim 2015). Wolves have been shown to limit moose populations through predation on calves (Testa et al. 2000*b*, Bertram and Vivion 2002).

Wolf predation accounted for 36% of adult moose mortalities in this study area during 2013–2016, yet ≥40% of cases exhibited health issues possibly predisposing them to predation (e.g., winter tick infestation, encephalitis, pneumonia; Carstensen et al. 2017). Health issues were the proximate cause of mortality for the remaining 64%. The overall poor health of the northeastern Minnesota moose population (Carstensen et al. 2015, 2017; DelGiudice and Severud 2017) could potentially explain not only the high number of capture-induced abandonments observed (DelGiudice et al. 2014, 2015), but also the high rates of predation on calves. Dams defended their calves less vigorously following harsh winters or if in poor nutritional condition in Alaska and Ontario (Keech et al. 2011, Patterson et al. 2013). In 2013, calf and adult survival were lowest (Severud et al. 2015*a*, Carstensen et al. 2017), and several adult mortalities resuled from winter tick infestation (Carstensen et al. 2017). Furthermore, >30% of snow-urine samples in winter 2013 were indicative of population-wide severe nutritional restriction, the highest incidence from 2013 to 2017 (DelGiudice and Severud 2017). All of these factors may have contributed to the population decline and low moose numbers, but it is still unclear what initiated the downward trajectory.

I predicted intrinsic factors may predispose calves to various sources of mortality, yet Cox proportional hazard models failed to detect any measurable effects on survival. Proximity between cow and calf may be important for survival, but not adequately assessed with current technology (e.g., collar linear error, location schedules dictated by

battery life) or my limited sample. Previous studies have failed to find that calf sex, litter size, dam age, or birth-date influenced survival (Franzmann and Schwartz 1986, Larsen et al. 1989, Ballard et al. 1991, Schwartz and Franzmann 1991, Ballard 1992). There is some evidence that litter size effects may disappear at high levels of mortality (Testa et al. 2000*b*, Bertram and Vivion 2002), but Keech et al. (2011) reported higher singleton than twin survival across wide ranges of overall calf survival and predation pressure. Keech et al. (2011) concluded that mortality of moose calves was largely independent of calf condition during high levels of predation pressure, because predators had few alternatives. Patterson et al (2013) found slightly higher survival for heavier calves at capture, but only for calves that died of non-predation causes. In cases where intrinsic factors were not shown to affect survival, habitat characteristics had a more pronounced effect via facilitation of predator search efficiency or deficient nutrition for lactating mothers (Jacques et al. 2015).

Calving habitat may be an important determinant of neonatal survival (Bowyer et al. 1999, Poole et al. 2007, Jacques et al. 2015). Generally, I observed mortalities to occur once dams and their calves departed calving sites, consistent with other studies that found calves are rarely killed at calving sites (Bubenik 2007). Previous studies have found much variability in habitat types used by cows for calving and during post-parturition (Leptich and Gilbert 1986, Addison et al. 1990, McGraw et al. 2012), but have generally agreed that cows tradeoff forage for predator avoidance (Bowyer et al. 1999, Testa et al. 2000*a*). However, there is risk to either movement or remaining cryptic (Lima and Dill 1990). Peak energetic demands for dams due to lactation occur 21–31

days postpartum (Schwartz and Renecker 2007), which coincides with the highest hazard calves experienced. This suggests that dams seeking out high quality or quantities of forage to meet this demand may be travelling in areas that expose their young calves to greater risk of predation, or that the movement itself increases that risk (Lima and Dill 1990, Frair et al. 2007). Earlier behavioral observations have concluded that once the dam and calf begin moving from the calving site, the likelihood of calves being killed increases, because the foraging dam frequently leaves the calf bedded (Bubenik 2007). My proximity data show calves spending more time away from dams as summer progresses, coincident with weaning and calves incorporating more forage into their diets.

Collared calves slipped their collars at a high rate in 2014 and to a lesser degree in 2013. Calves that slipped their collars were later assessed for survival during winter survey flights, which allowed slight adjustments to annual survival estimates. Similarly, uncollared calves in 2015 were assessed for survival twice throughout the winter. A calf no longer associated with its dam during surveys in 2015 was presumed dead (Berger 2012). Proximity data showed close association of dams and calves throughout winter (indicating I was likely to see calves during surveys); however, 1 calf did survive after being separated from its dam and twin. Although surveys yielded coarse survival estimates, the exact timing, cause of mortality, and initial litter size were unknown. I treated lone cows that made a calving movement the previous spring as losing a single calf, resulting in 2015 survival estimates that are likely biased high.

In 2013 and 2014, I conservatively censored 20 neonates from survival analyses due to capture-related mortality. In some cases (e.g., calf not nursing), the neonate was unlikely to survive in the absence of collaring activities. In other cases, capture and handling more likely caused (e.g., dam trampling calf) or contributed to mortality (e.g., abandonment). Capture-induced abandonment is poorly understood, but there is some evidence that more viable calves (i.e., those that moved farther from capture-sites post-handling) were less likely to be abandoned (DelGiudice et al. in press, 2015). Removing these 20 individuals likely violated the assumption that censoring was independent of fate and biased my survival rates high.

Calving movements were a reliable method to indicate calving in all 3 years of the study. Use of this behavior, coupled with specific locations from the GPS collars, allowed me to locate neonates for capture, estimate timing of births, and investigate calving sites. Furthermore, mortality movements by dams have shown much promise in determining the timing and cause of calf deaths. These indirect methods can be used to answer some questions relative to management, but still leave others unanswered (i.e., twinning rates). Additionally, these non-invasive methods (relative to calves) still required GPS-collaring of adult females to be possible. Using GPS collars on calves to estimate survival and cause-specific mortality was far superior to using movement to infer neonatal status. Examining capture-induced abandonment, non-predation mortalities, and fine-scale habitat use were all greatly facilitated using GPS collars.

MANAGEMENT IMPLICATIONS

Predator control has often been invoked as a management strategy to increase ungulate populations. In this case, I observed high rates of predation on calves, yet underlying health issues for adults at the population level are still evident, so it is unclear if predator reduction would result in overall population growth. Wolves are currently state- and federally protected in Minnesota. The remaining major predator of calves that could possibly be managed is bears, yet their effect on calf survival was minimal compared to wolves.

Habitat restoration leading to improved nutritional status of adults may lead to higher survival of calves (Keech et al. 2011, Patterson et al. 2013). Directed projects that target specific habitat types used by moose during unique life stages (i.e., calving, lactation, winter) may be more fruitful than broad-scale landscape manipulations.

As of publication, the executive order that barred collaring of moose in Minnesota still stands. Northeastern Minnesota's moose population, although recently showing signs of stabilization, is still markedly reduced compared to 2006 (DelGiudice 2017). Northwestern Minnesota's population exhibited similar intermittent short-term intervals of apparent stability before ultimately becoming functionally extirpated (Murray et al. 2006, Lenarz 2007). I have made strides in gleaning information about calves indirectly from GPS-collared adults, yet attrition of those collars is ongoing due to mortalities and battery-life expiration. Data obtained from placement of collars on free-ranging animals is still a critical tool in the wildlife biologist's armamentarium. Without it, I am limited in what inferences I can make about specific mechanisms behind population changes.

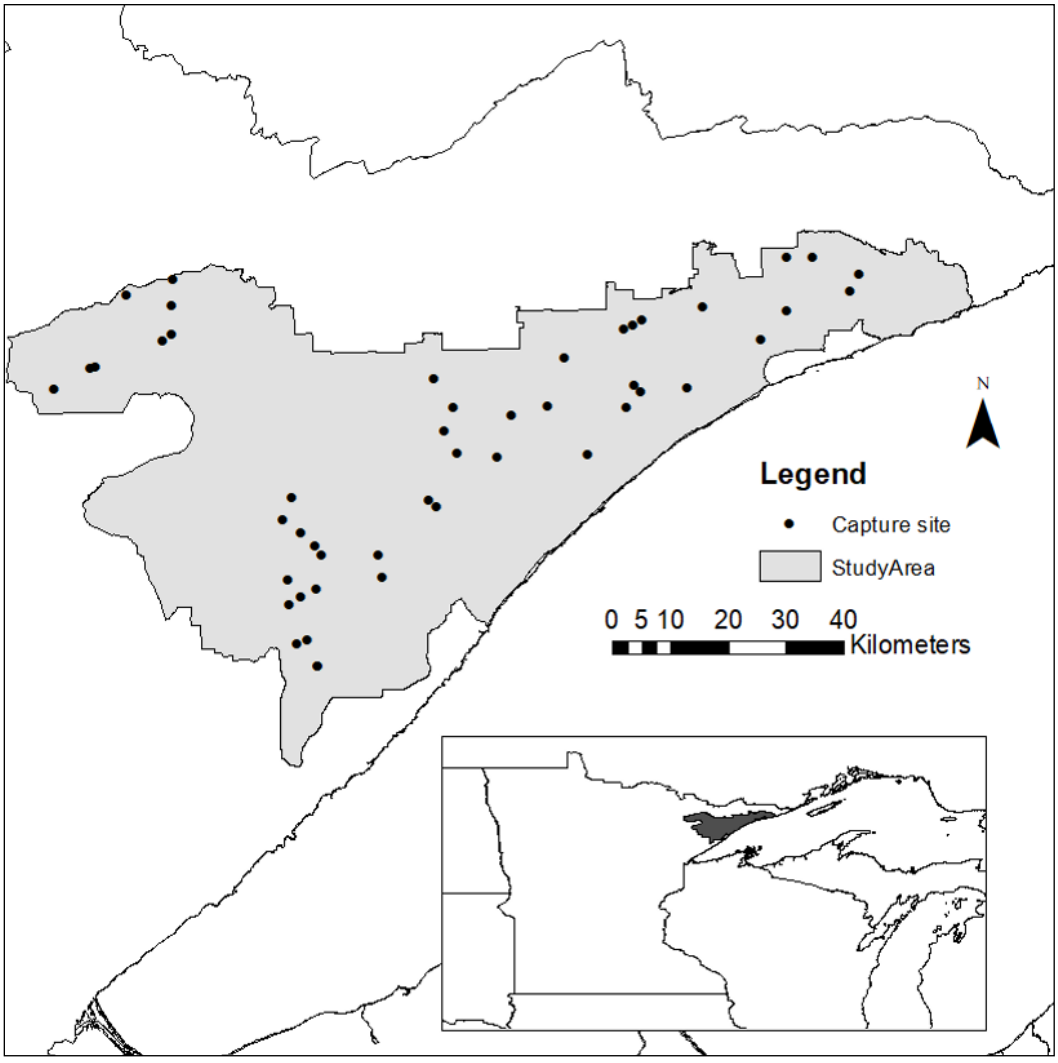

Figure 1. Capture sites of moose neonates (n = 74; 6,068 km^2-study area), May–June 2013–2014, northeastern Minnesota.

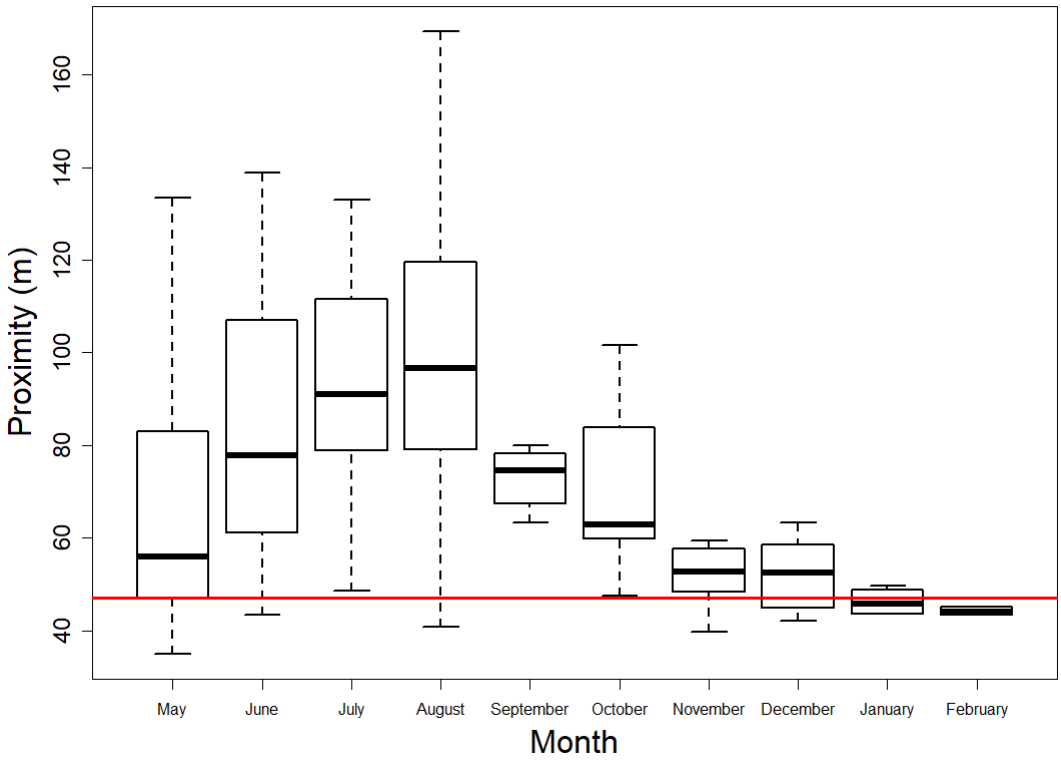

Figure 2. Monthly proximity (m) between moose dams and calves (*n* = 161 dam-calf months), May–February 2013–2105, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, and whiskers are 1.5× interquartile range. Horizontal red line depicts cumulative mean linear error associated with calf and adult GPS collars (7 m for adult collars, 40 m for calf collars, totaling 47 m).

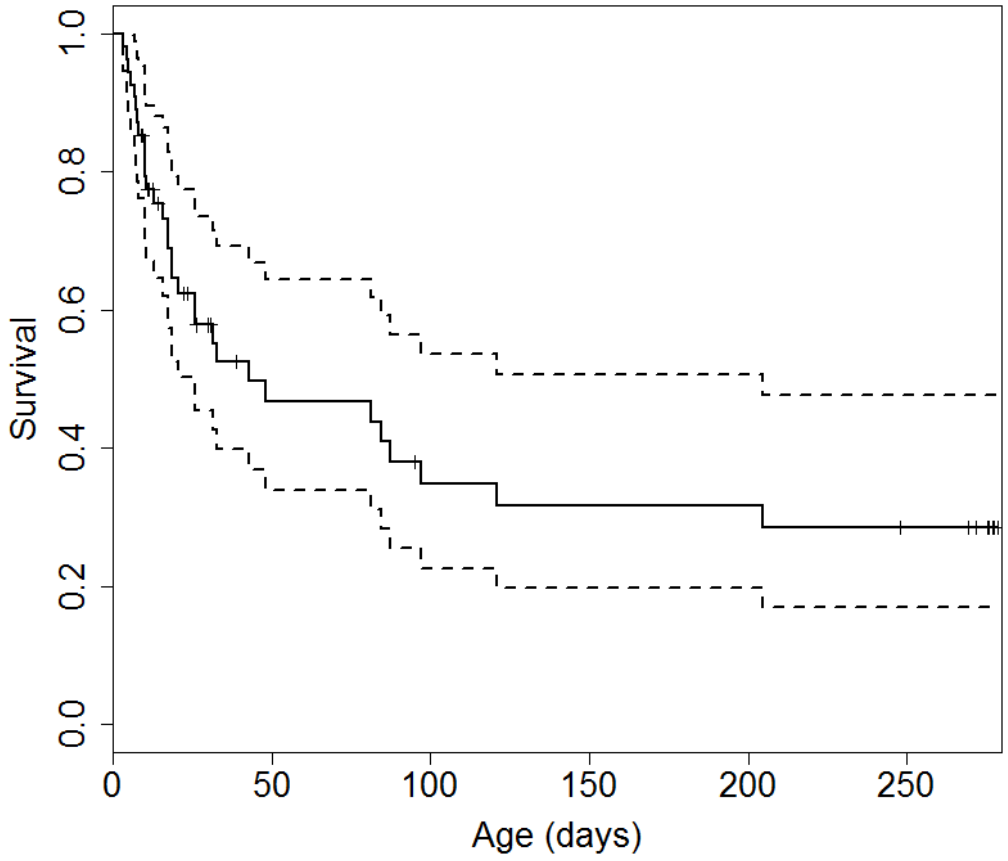

Figure 3. Kaplan-Meier 250-day survival for known moose calf fates (*n* = 54 calves), May–February 2013–2015, northeastern Minnesota. Tick marks indicate individuals censored due to slipped or removed collars. Dashed lines represent 95% confidence intervals.

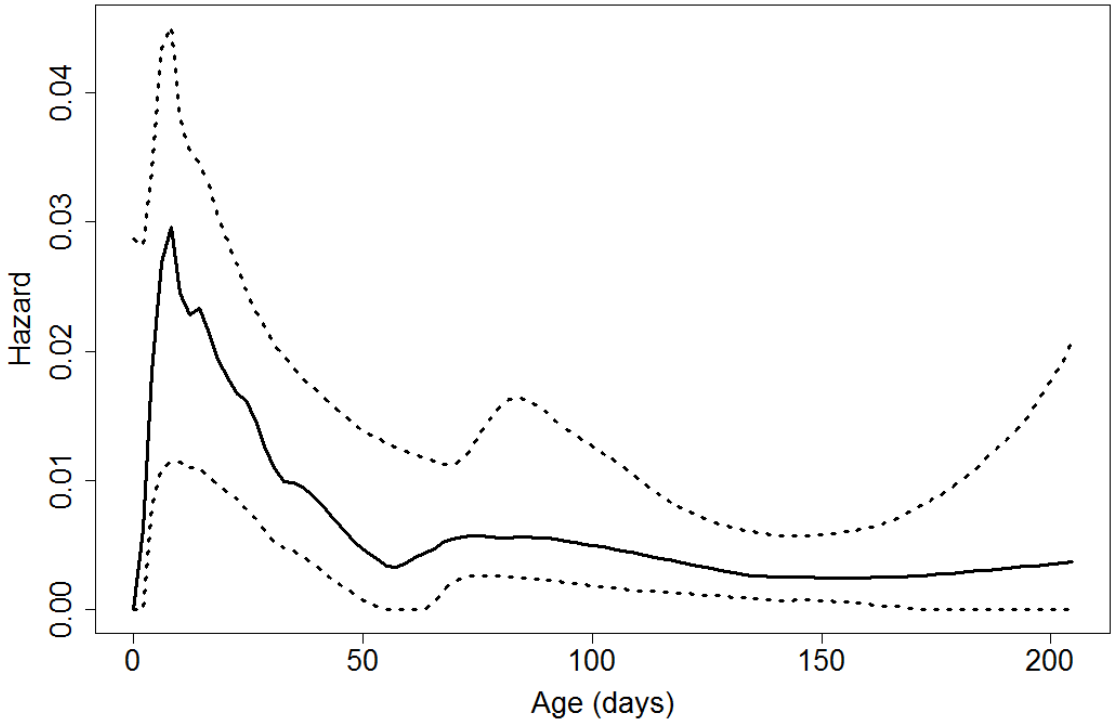

Figure 4. Empirical hazard function for known moose calf fates (n = 54 calves), May–February 2013–2015, northeastern Minnesota. Dashed lines represent 95% confidence intervals.

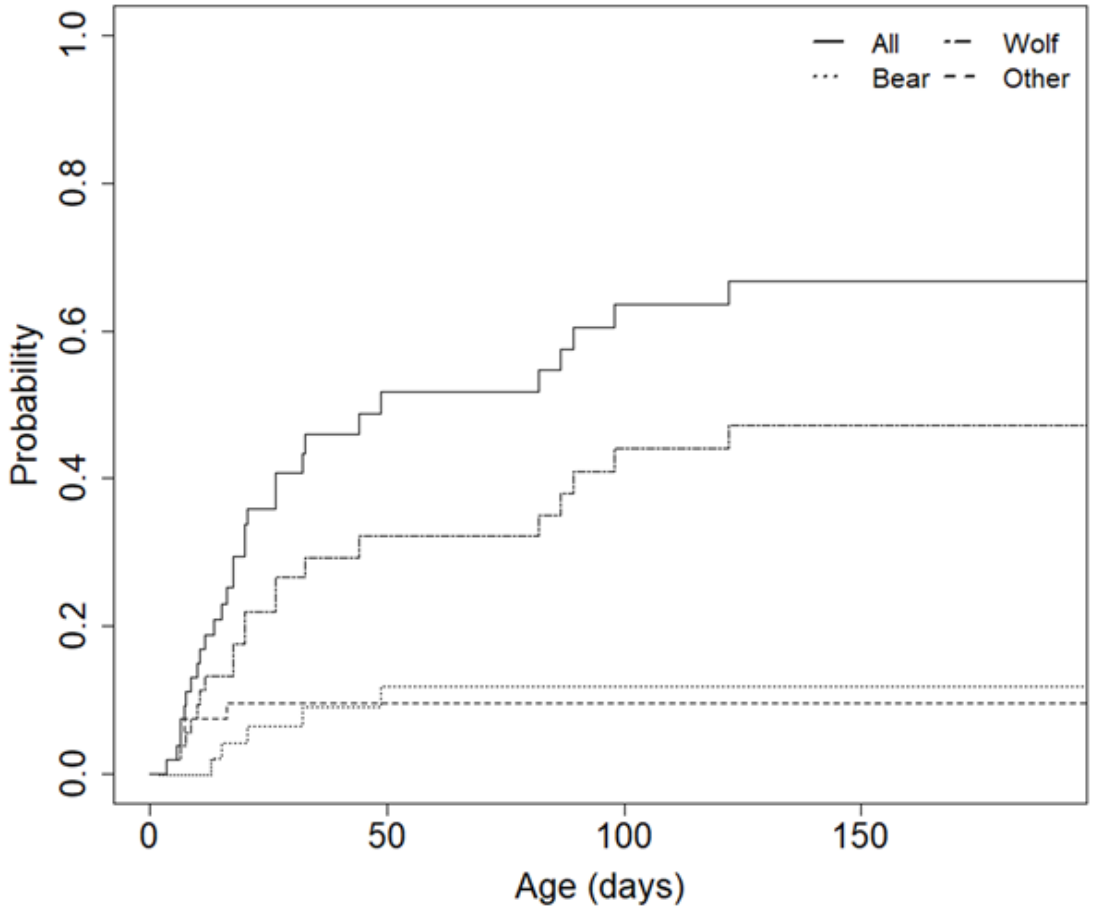

Figure 5. Cumulative incidence function for cause-specific mortality of moose calves (*n* = 40 calves), May–February 2013–2015, northeastern Minnesota. Causes of mortality were wolf predation (20), black bear predation (5), and other (natural abandonment [2], drowning [1], abandonment of unknown cause [1], unknown predator [1], and infection resulting from wolf attack [1]).

Chapter 3: Association of Moose Parturition and Post-parturition Habitat with Calf Survival

ABSTRACT Habitat use during calving and the energetically demanding post-parturition period can be an important determinant of neonatal survival. The moose (*Alces alces*) population in northeastern Minnesota has declined 58% from 2006 to 2017. During 2013–2015, annual survival of calves was estimated as low as 28%. I remotely monitored global positioning system (GPS)-collared adult female moose and neonates during the calving and post-parturition seasons to examine calving movements, birth-sites, habitat use, survival and cause-specific mortality of neonates. I surveyed and compared habitat characteristics of pre-calving, calving, peak-lactation, and mortality sites at a fine and broad scale. I also compared mortality sites of kills by wolves (*Canis lupus*) and other mortality sources, as well as calving sites of cows that successfully reared a calf to winter to those that did not. Cows tended to move to areas of more conifer forest cover to calve. During peak-lactation, cows and their calves used steeper areas with abundant forage, high concealment, and less conifer cover. Mortalities occurred at sites that were more level than other site types. Generally, wolf-kill sites were farther from roads. Cows that successfully reared a calf to winter typically calved in areas with more deciduous forest and less forested wetland cover than cows whose calves died. Habitat improvement projects for moose should consider not only forage requirements, but also cover, slope, and road density. Identifying the association of specific landscape characteristics with neonate survival should yield insight into

mechanisms contributing to the declining moose population and serve as a basis for an ecologically sound management response.

INTRODUCTION

Variable juvenile survival can have profound impacts on ungulate population dynamics (Gaillard et al. 1998, 2000; Raithel et al. 2007). Calving and post-parturition habitat can greatly affect neonatal survival (Jacques et al. 2015). Often females trade off access to forage for predator avoidance during this vulnerable life stage (Bowyer et al. 1999, Poole et al. 2007, Pinard et al. 2012, Pitman et al. 2014). Forage availability can affect how well females replenish fat stores after the nutritional restriction of winter, yet quality patches may be located in areas frequented by predators (Edwards 1983, Creel et al. 2005). Hiding cover, landscape heterogeneity, and linear features may affect detection by predators and consequently vulnerability to predation (Stephens and Peterson 1984, Griffith and Youtie 1988, Kauffman et al. 2007, Karsch et al. 2016, Gulsby et al. 2017).

Cow moose (*Alces alces*) use a variety of cover types for calving, often in proportion to their availability (Addison et al. 1990, Bowyer et al. 1999, Poole et al. 2007), yet some studies have observed selection for specific cover types used in post-parturition areas, such as lowland conifer, shrublands, and regenerating forest (McGraw et al. 2012). Peninsulas and islets may offer protection from predators, but also may only be used in proportion to availability (Stephens and Peterson 1984, Addison et al. 1990). Since moose occupy various landscapes throughout their geographic range, available habitat differs vastly (Timmermann and Rodgers 2017). Recently in northeastern Minnesota (2013–2015), few calf mortalities were observed at calving sites (Severud et

al. 2017), similar to observations elsewhere (Bubenik 2007). Moose, as well as elk (*Cervus elaphus*), may use anthropogenic features as shields against predators, calving near roads or campsites that predators often avoid (Edwards 1983, Lehman et al. 2016). Moose calving sites have exhibited predator-avoidance characteristics such as increased visibility to detect approaching predators, associated with either higher elevation, steeper slopes, or lower tree density (Addison et al. 1990, Wilton and Garner 1991, Bowyer et al. 1999, Poole et al. 2007).

As nutritional demands for lactation increase, and rapidly growing calves begin to browse, forage may become more important than predator avoidance for both dams and calves. Additionally, calf mobility increases, allowing juveniles to better keep up with their mothers and evade predators (Altmann 1958). Lactation is a high energy-demanding phase of reproduction for mammalian mothers, requiring 2–3× more energy than gestation (Robbins 1993). Milk production peaks 21–31 days post-parturition for moose cows (Schwartz and Renecker 2007). Habitat selection by dams during this time is driven primarily by the need for abundant forage (Belovsky 1978, Thompson and Stewart 2007); however, cows with calves-at-heel selected habitats that provided protection from predation rather than higher amounts of forage during spring and summer (Dussault et al. 2005). Experimental food restriction of white-tailed deer (*Odocoileus virginianus*) during lactation found fawns gained less mass, nursed more, and spent more time with their mothers foraging (Therrien et al. 2008). Furthermore, fawn survival decreased 35% (Therrien et al. 2007). Lactating red deer (*Cervus elaphus*) spent more

time grazing on high quality forage and moved less than non-lactating hinds during spring and summer (Clutton-Brock et al. 1982).

Wolves (*Canis lupus*) prey on adult and calf moose where the 2 species are sympatric (Peterson 1999, DelGiudice et al. 2009, Keech et al. 2011, Severud et al. 2015*a*). Adult moose are formidable prey of wolves, often standing their ground rather than fleeing when approached by wolves (Mech et al. 2015); however, calves are vulnerable to predator attack especially during their first summer (Patterson et al. 2013, Severud et al. 2015*a*). Hunting behavior of wolves often involves "coursing," but they have been observed or inferred to use thick vegetation to stalk and ambush prey as well (Kunkel and Pletscher 2001, Mech et al. 2015, Gable et al. 2016). To maximize travel speed and prey-encounter rates, wolves use drainages, rivers, edges, and natural and anthropogenic linear features as travel corridors (Kunkel and Pletscher 2001, Latham et al. 2011, Whittington et al. 2011).

Northeastern Minnesota's moose population has declined 58% from 2006 to 2017 (DelGiudice 2017), during which time annual calf survival has been estimated between 0.28 and 0.40 (Lenarz et al. 2010, Severud et al. 2017). Patterns of calving and post-parturition habitat use and its association with neonatal survival were largely unknown. I investigated cow habitat use before, during, and after calving at 2 scales of spatial resolution. My objectives were to assess differences in habitat characteristics at pre-calving, calving, peak-lactation, and mortality sites. I further assessed differences in mortality sites by mortality cause, and differences in calving sites of cows that successfully reared a calf to winter versus those that did not. I predicted that female

moose would tradeoff forage availability for predator avoidance during calving, but energetic demands of lactation would outweigh predator avoidance post-parturition. Specifically, I predicted dams would use calving sites with lower amounts of forage, yet more concealment cover for calves and greater visibility for the dam to detect oncoming predators. Second, I predicted cows would use areas with more forage during peak lactation, and mortality sites would have low concealment and visibility. Third, because wolves are known to use linear features and habitat edges to search for prey, I predicted that wolf-kills would occur closer to linear features and in more heterogenous habitat compared to other forms of mortality. Finally, I predicted calf survival would be higher at birth-sites with more forage availability and concealment.

STUDY AREA

I conducted this study in northeastern Minnesota along the southern extent of moose range in North America (Lenarz et al. 2010, Timmermann and Rodgers 2017). A mosaic of the Superior National Forest and various state, county, and private lands, the area comprised 6,068 km^2 between 47°06'N and 47°58'N latitude and 90°04'W and 92°17'W longitude. State and tribal moose harvest was suspended in 2013 due to the steady population decline (DelGiudice 2012). This region has been characterized as the Northern Superior Upland, within the Laurentian mixed forest province (Minnesota Department of Natural Resources [MNDNR] 2015). Timber harvest declined from 2001 to 2013 (Wilson and Ek 2013). Vegetation is a mixture of wetlands, lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*), and upland stands of balsam fir (*Abies balsamea*), jack pine (*Pinus*

banksiana), white pine (*P. strobus*), and red pine (*P. resinosa*). The uplands also contain trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) within the conifer stands.

Predators of moose calves were gray wolves and American black bears (*Ursus americanus*; (Lenarz et al. 2009; Patterson et al. 2013; Severud et al. 2015*a*, *b*); wolf and bear densities were estimated at 4.4/100 km^2 and 23/100 km^2, respectively (Mech et al. in press, Garshelis and Noyce 2011). White-tailed deer, managed at pre-fawning densities of <4/km^2, were primary prey of wolves in the area (Nelson and Mech 1981, DelGiudice et al. 2002, Minnesota Department of Natural Resources 2012). Alternate wolf prey included beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), black bears, and various small mammals (Stenlund 1955, Frenzel 1974, Van Ballenberghe et al. 1975, Chenaux-Ibrahim 2015).

METHODS

Moose Captures

Adult and calf moose were GPS-collared as part of the MNDNR's survival and cause-specific mortality studies (Severud et al. 2015*a*, Carstensen et al. 2017). Adult female and calf collars collected hourly locations during May and June (calving season). I monitored 193 cows (73 in 2013, 70 in 2014, and 50 in 2015) and 139 calves (49 collared in 2013, 25 collared in 2014, ~65 uncollared calves remotely monitored in 2015; Severud et al. 2017). Details of moose capture and collar specifics were described elsewhere (Butler et al. 2013; Carstensen et al. 2015, 2017; Severud et al. 2015*a*; Obermoller et al. 2017).

Fine-scale Habitat Assessment

In 2015, I recorded site characteristics at pre-calving and calving sites (averaged GPS coordinates over a 40- to 48-hour period immediately following the calving movement, adjusted on site as confirmed by calving evidence; Fig. 1). I used starting and ending points of calving movements to identify pre-calving and calving sites, respectively (Severud et al. 2015*a*). I similarly surveyed locations where calf mortalities were confirmed by site evidence (e.g., bone fragments, hooves, hair, or predator sign) following a mortality movement of the dam, because neonates were not collared in 2015 (Severud et al. 2015*b*, Obermoller et al. 2017). Mortalities occurring at the birth-site were recorded as both calving and mortality sites. When mortalities occurred outside of the birth-site, new habitat data were collected.

In 2015, when I observed evidence indicating a given calf had survived ≥26 days (pellets and tracks, continued reduction in dam movement), I recorded site characteristics at the corresponding cow's peak-lactation location (26 days post parturition). If the location was in the middle of a long movement, I used the center of the nearest grouping of ≥3 locations, typically 1 hour apart. I conducted all habitat surveys to match phenological conditions (i.e., leaf-off and leaf-on) to the time the initial location was used by the moose. All sites were surveyed once the dam and calf or calves had departed.

Habitat plots were centered at each cow's GPS location closest to the time of interest, unless that location was refuted by visual evidence. This typically occurred at calving and mortality sites when calving beds or kill-sites were readily observed. In these cases, plot centers were placed in the middle of the cow's calving bed or at the

primary location of calf remains or sign of a struggle. An average waypoint was recorded in the center of each plot using a handheld GPS unit, and I recorded the elevation from the unit's base map, and used a spherical convex densiometer to estimate canopy density (%). I also measured the prevailing slope (%) and aspect (°) using a clinometer and compass.

Canopy density (in addition to being measured at the plot center) and horizontal visibility were recorded 15 m from the plot center in each cardinal direction. The mean and standard deviation of the 5 canopy measurements were calculated. I used a 2-m cover pole to determine horizontal visibility, recording the visible percentage (0, 25, 50, 75, or 100%) of each of 19 bands from the center of the plot (Poole et al. 2007). Mean and standard deviation of visibility were then calculated. A cardboard cut-out of a standing moose calf silhouette was held at the center of the plot and I recorded the percentage of the cut-out that an observer could see from 15 m at a 1-m height in each cardinal direction to estimate calf visibility (low values reflect less of silhouette visible meaning higher concealment). The observer then moved towards the cut-out, maintaining a 1-m height, and recorded the distance from the calf when visibility reached 25, 50, 75, and 100%. I then calculated mean visibility and standard deviation for each plot.

I recorded trees, saplings, and shrubs within an 11-m radius from the central point. Trees were defined as any upright (<45° lean) woody plant with a diameter at breast height (DBH) ≥10 cm. Saplings and shrubs were defined as DBH <10 cm. I determined the species and DBH of each tree, alive or dead, and counted number of

stems of saplings and shrubs by species. Living trees <18 cm DBH and shrubs were further classified as forage or non-forage species (Peek et al. 1976, Portinga and Moen 2015).

Broad-scale Habitat Assessment

To investigate broad-scale patterns, I buffered pre-calving, calving, peak-lactation, and mortality sites from 2013–2015 (sites defined using the same criteria listed above) with a 565-m radius to expand plots to about 100 ha (Poole et al. 2007, McGraw et al. 2012). I overlaid these circular plots on a land-cover-classification layer (Minnesota Land Cover Classification and Impervious Surface Area by Landsat and Lidar) and calculated the proportion of each cover-class. I also calculated the amount of edge within the buffers, distance to edge, road density, and distance to road. I used road, trail, and snowmobile trail layers (manmade linear features, hereafter "roads"), then summed road length (km) and divided by area (km^2) to calculate road density. I delineated edge using Geospatial Modelling Environment (Beyer 2015); all other analyses were conducted in ArcGIS version 10.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA).

Statistical Analyses

I used a cluster bootstrapped analysis of variance (ANOVA) to compare habitat characteristics by site types (pre-calving, calving, peak-lactation, and mortality). To account for non-independence of observations obtained from the same moose and unbalanced design (i.e., individual moose had observations ranging from 1 to all 4 site types), I created 10,000 bootstrapped samples of the data in which clustered observations associated with individual moose were sampled with replacement. I used these

bootstrapped samples to estimate the distribution of an *F* statistic under a null model that all means were equal for each site type. For each habitat characteristic, I shifted each observation by subtracting the sample mean of its site type and then added the overall sample mean such that the means of each site type were all equal to the overall sample mean. I computed a bootstrapped *P*-value for the *F* statistic associated with the original data by counting the proportion of bootstrapped *F* values that were larger than the observed *F* statistic. I concluded there was an effect of site type on that specific variable if $P < 0.05$. I also created a bootstrapped distribution of *t* statistics for all pairwise comparisons under the null model. If the bootstrapped ANOVA showed a significant effect of site type, I examined pairwise comparison *t* statistics. If the *t* statistic associated with the original data fell below the 2.5^{th} quantile or above the 97.5^{th} quantile of the bootstrapped *t* statistics under the null model, then a significant difference existed between the pair of examined site types. I compared calving sites of surviving and non-surviving calves and mortality sites of wolf-kills and other causes using linear models.

RESULTS

Fine-scale Habitat Assessments

I measured fine-scale habitat characteristics at 34 pre-calving, 37 calving, 25 peak-lactation, and 10 mortality sites in 2015. Linear models indicated significant variation by site type for slope (Fig. 2, $P = 0.03$), mean calf visibility at 15 m (Fig. 3, $P = 0.02$), and mean canopy closure (Fig. 4, $P = 0.04$). Post hoc comparisons for slope indicated mortality sites were flatter than all other site types ($P \leq 0.01$), and calving sites were flatter than peak-lactation sites (Fig. 2, $P = 0.04$). Calf visibility at 15 m was lowest at

peak-lactation sites compared to pre-calving and calving sites ($P \leq 0.005$), but was not different from mortality sites (Fig. 3, $P = 0.10$). Peak-lactation sites had denser canopy closure compared to pre-calving and calving sites ($P \leq 0.02$), but did not differ from mortality sites (Fig. 4, $P = 0.06$). Although peak-lactation sites contained nearly twice as much forage compared to all other site types (Fig. 5), this was not statistically significant ($P = 0.16$). Slope should be interpreted cautiously due to small differences in slope ($\overline{x}_{\text{peak-lactation}} = 10.1\%$ vs. $\overline{x}_{\text{mortality}} = 3.5\%$; Fig. 2). Fine-scale habitat variables were similar between calving sites of dams of surviving versus non-surviving calves.

Broad-scale Habitat Assessment

I analyzed 150 pre-calving, 155 calving, 73 peak-lactation, and 36 mortality sites from 2013 to 2015. Only 3% of parturient cows did not make a calving movement, but I confirmed calving via direct observation of a calf or site evidence. Cows that retained a calf-at-heel 26 days postpartum were included in peak-lactation surveys. I also compared 24 wolf predation sites to 12 mortality sites of other causes (bear predation, unknown predation, drowning, natural abandonment, infection). I again compared calving sites of cows that successfully reared ≥1 calf to winter ($n = 10$) to calving sites of cows that lost calves to mortality ($n = 30$).

Sites did not differ by any landcover or heterogeneity measures, except for coniferous forest (Fig. 6, $P = 0.006$). Calving and mortality sites contained more conifer cover than pre-calving and peak-lactation sites (Fig. 6, $P \leq 0.012$). Calving sites of dam of surviving calves contained nearly twice as much deciduous forest ($F_{1,38} = 10.33$, $P = 0.003$), but about one-fourth the amount of forested wetlands than dams of non-surviving

calves ($F_{1,38}$ = 7.80, P = 0.008; Table 1). Wolf predation sites were over 2× farther from roads than non-wolf mortality sites ($F_{1,38}$ = 4.61, P = 0.040; Fig. 7; Table 2). Road density within buffers of non-wolf mortality sites was 113% higher than at wolf mortality sites ($F_{1,38}$ = 5.26, P = 0.030; Table 2).

DISCUSSION

Ungulates typically tradeoff forage availability for avoidance from predators during vulnerable life stages, such as calving. As predicted, results suggested calving sites contained higher amounts of non-forage cover type (conifer forest) yet more calf visibility (compared to peak-lactation sites). This is consistent with previous reports of moose cows using areas with less forage to calve (Bowyer et al. 1999, Poole et al. 2007). Use of GPS-collared cows facilitated the use of fine-scale data to locate calving beds and mortality sites. The collars also allowed me to observe dam and calf localization for up to 2 weeks post-parturition (McGraw et al. 2014, Severud et al. 2015*a*) and proximity (monthly mean <70 m) for up to 9 months (Severud et al. 2017). Localization at calving sites can be so extreme and the amount of forage so lacking that I occasionally observed bark-stripping, a sign of severe nutritional deprivation (Miquelle and van Ballenberghe 1989).

Calving sites in my study area were relatively safe from predators (Severud et al. 2017). A plausible explanation for this may be slightly higher road densities near calving sites, as has been observed with elk (*Cervus canadensis nelsoni*) and moose in other areas (Stephens and Peterson 1984, Lehman et al. 2016). Wolf predation was the leading cause

of calf mortality in this area (Severud et al. 2017), and wolf-kills occurred farther from roads than other forms of mortality, indicating that roads may act as a "shield."

As predicted, dams moved into areas with more available forage when lactation demands peaked. Although this difference was not statistically significant, I considered it biologically significant. This increase in forage was revealed at both a fine (more forage stems, greater concealment cover, and higher canopy closure) and a broad scale (less conifer cover). Collared moose in Finland showed a similar pattern; cows calved in areas with minimal vegetation <5 m in height, but cows and their calves moved to areas with dense vegetation shortly thereafter, ostensibly to seek out high quality and quantities of forage (Melin et al. 2015). Lactation is 2–3× more energetically costly than gestation, and lactating cows require 65–125% more energy than non-lactating females (Robbins 1993). Nursing twins versus a singleton increases this cost about 67% (Schwartz and Renecker 2007). Lactation increases daily protein requirements for moose 10–14% (Schwartz and Renecker 2007). Peak-lactation usually coincides with peak vegetation abundance (Robbins and Robbins 1979). These pronounced increases in nutritional requirements underscore the importance of ample quality forage during lactation. However, other ungulates typically continue to avoid predation at the expense of access to forage while juveniles are at-heel (Pitman et al. 2014, Smith et al. 2015, Karsch et al. 2016). Northeastern Minnesota's moose population may be nutritionally stressed in winter to the extent that dams and their calves must then contend with the greater predation risk (DelGiudice and Severud 2017), and possibly decreased calf survival. Cow moose in Norway that used mixed forest landcover (preferred forage habitat) in

winter were in better condition at parturition and experienced increased calf survival (Allen et al. 2017).

I predicted cows that calved in areas with abundant forage and high concealment to hide calves from predators would exhibit higher calf survival. Calf visibility did not differ among pre-calving, calving, or mortality sites, but was lower at peak-lactation sites. Wolves and bears may depend more on olfaction or chance encounter rather than vision to locate prey (Bastille-Rousseau et al. 2011, Mech et al. 2015). In my study, cows that calved in areas with more deciduous forest, indicative of good foraging habitat (Mabille et al. 2012), were more likely to rear a calf to winter. Conversely, calving sites in areas with higher amounts of forested wetlands were associated with lower calf survival. Since concealment cover was often vegetative (i.e., small diameter conifers, large diameter trees), locations on the landscape that offer abundant forage *and* concealment pre-leaf-out may be rare. Cows that calve in deciduous forest may have sufficient quality forage available without requiring increased movement and associated predation risk, can therefore recover nutritionally while localized with their calf. If forage availability is associated with less movement (Saïd and Servanty 2005), detection by predators may be reduced. This increase in nutrition may have facilitated a higher quantity and quality of milk and an increased ability of the dam to protect its calf from predators, since moose that are nutritionally stressed defend calves less vigorously (Keech et al. 2011, Patterson et al. 2013). A possible alternate explanation is that predators differentially use habitat types during this time of year (Hebblewhite et al. 2005, Bastille-Rousseau et al. 2011, DeCesare 2012).

Peak-lactation sites offered much more forage and greater concealment cover. However, these factors may limit visibility for the dam, potentially precluding her ability to detect approaching predators. Movement can increase detection by predators (Lima and Dill 1990, Frair et al. 2007), thus making dams and calves more vulnerable to predation (Stephens and Peterson 1984). Movement through thick forested cover may be even more dangerous. Wolves used vegetation (or were inferred to) to ambush prey in a variety of landscapes and seasons (Kunkel and Pletscher 2001, Gable et al. 2016). White-tailed deer preferred nutritious forage that regenerates after fire, but only if hiding cover was sufficient (Lashley et al. 2015). Peak-lactation sites had more forage stems and concealment, but I did not assess the nutritive value of the various plants at each site.

I predicted that mortality sites would have low calf concealment cover and obstructed dam views (horizontal visibility), and that, specifically, wolf-kill sites would be closer to roads and edges. Fine-scale analyses of mortality sites showed that calves died at flatter sites (more limited cow visibility). Hypothetically, moose moved to higher elevations for calving to be able to detect approaching predators (Wilton and Garner 1991, Poole et al. 2007). Greater detection distances increase the dam's ability to move off before being encountered.

Sample size precluded a fine-scale analysis, but at a broad scale, wolf-kills occurred farther from roads, contrary to my prediction. Wolves travel along drainages and habitat edges while searching for prey (Kunkel and Pletscher 2001; Whittington et al. 2005, 2011; Latham et al. 2011), and dam-calf groups foraging near edges may have been more detectable. Moose may flee to water when attempting to escape predation

(Stephens and Peterson 1984); however, based on hourly movement trajectories of GPS-collared dams and calves, there did not appear to be a pattern of chase by predators preying on calves. Evidence points to dams and calves being ambushed or not moving much if they do sense predators beforehand.

Road density of 0.6 km/km^2 has been used as a general threshold for wolf occurrence in the northern Great Lakes region (Thiel 1985, Mech et al. 1988), although a small number of packs in northern Minnesota were observed at densities >0.9 km/km^2 (Mech 1989, Fuller et al. 1992). Wolves may differentially use roads, trails, and railways, generally avoiding high-use linear features (Whittington et al. 2005). I observed wolf-kills of calves farther from roads, and generally, in areas of lower road density. The mean road density for all sites was 0.80 km/km^2, but wolf-kills occurred in buffers with a density of 0.58 km/km^2 (compared to 1.24 km/km^2 at non-wolf-kill mortality sites). The 100-ha buffers are a smaller scale than the township- or county-scale used when calculating road density, but still indicated an influence on wolf predation. I did not analyze by intensity of road use due to sample-size limitations, but the general pattern of wolf-kills occurring farther from roads persisted. Wolves were harvested in this region in November–December 2012 and 2013 (Stark and Erb 2014), immediately prior to and during this study. Wolf avoidance of roads in response to harvest has been documented (Thurber et al. 1994).

MANAGEMENT IMPLICATIONS

Northeastern Minnesota's moose population decline has prompted many habitat restoration projects by well-meaning groups committed to moose persistence in the

region. My research may serve as a guide for planting species that may increase calf survival, such as deciduous and mixed forest species most palatable to moose. These foraging areas should be close to areas of dense concealment cover in which cows and calves can hide during calving, and within an existing road-density framework that may deter wolf predation. Since calving generally occurs pre-leaf-out, dense concealment cannot be achieved with deciduous shrubs and saplings, but rather requires small-diameter conifers and topography. Managing foraging areas on slopes >4% might allow cows to more easily detect approaching predators and better defend their calves. There is recent evidence that winter forage may be limited in the study area, subjecting moose to varying incidences of severe winter nutritional restriction (DelGiudice and Severud 2017). Assuring that pregnant cows exiting winter in compromised body condition have access to calving areas with plentiful forage and concealment cover may contribute to increased calf recruitment.

Table 1. Broad-scale land-cover type proportions of buffered areas surrounding calving sites of dams that successfully reared a calf to winter ("Survivors," *n* = 10) versus those that did not ("Non-survivors," *n* = 30), 2013–2015, northeastern Minnesota.

	Survivors		Non-survivors				
	$\overline{x}$	SE	$\overline{x}$	SE	*F*	df	*P*
Forested wetland	0.06	0.01	0.23	0.03	7.80	1,38	0.008
Deciduous forest	0.39	0.06	0.14	0.04	10.33	1,38	0.003

Table 2. Broad-scale road metrics within buffered areas surrounding mortality sites of wolf-killed calves (n = 24) and calves that died of other causes (n = 12), 2013–2015, northeastern Minnesota.

	Wolf predation		Other cause				
	$\overline{x}$	SE	$\overline{x}$	SE	F	df	P
Distance to road (m)	804	139	368	67	4.61	1,34	0.04
Road density (km/km^2)	0.58	0.15	1.24	0.27	5.26	1,34	0.03

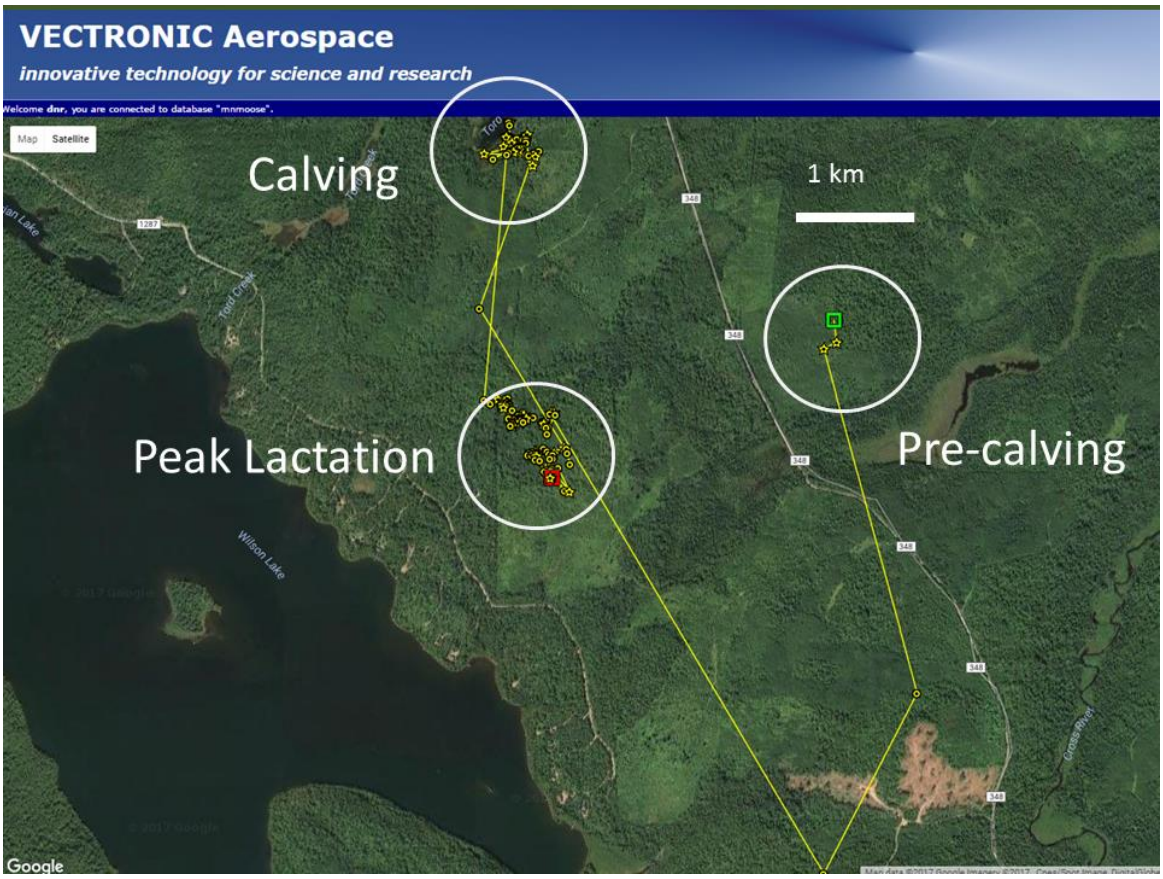

Figure 1. Example of moose pre-calving, calving, and peak-lactation sites, May–July 2013–2015, northeastern Minnesota. Pre-calving sites were defined as the origin of the calving movement; peak-lactation sites were locations of dams 26 days post-parturition (milk production peaks 21–31 days postpartum).

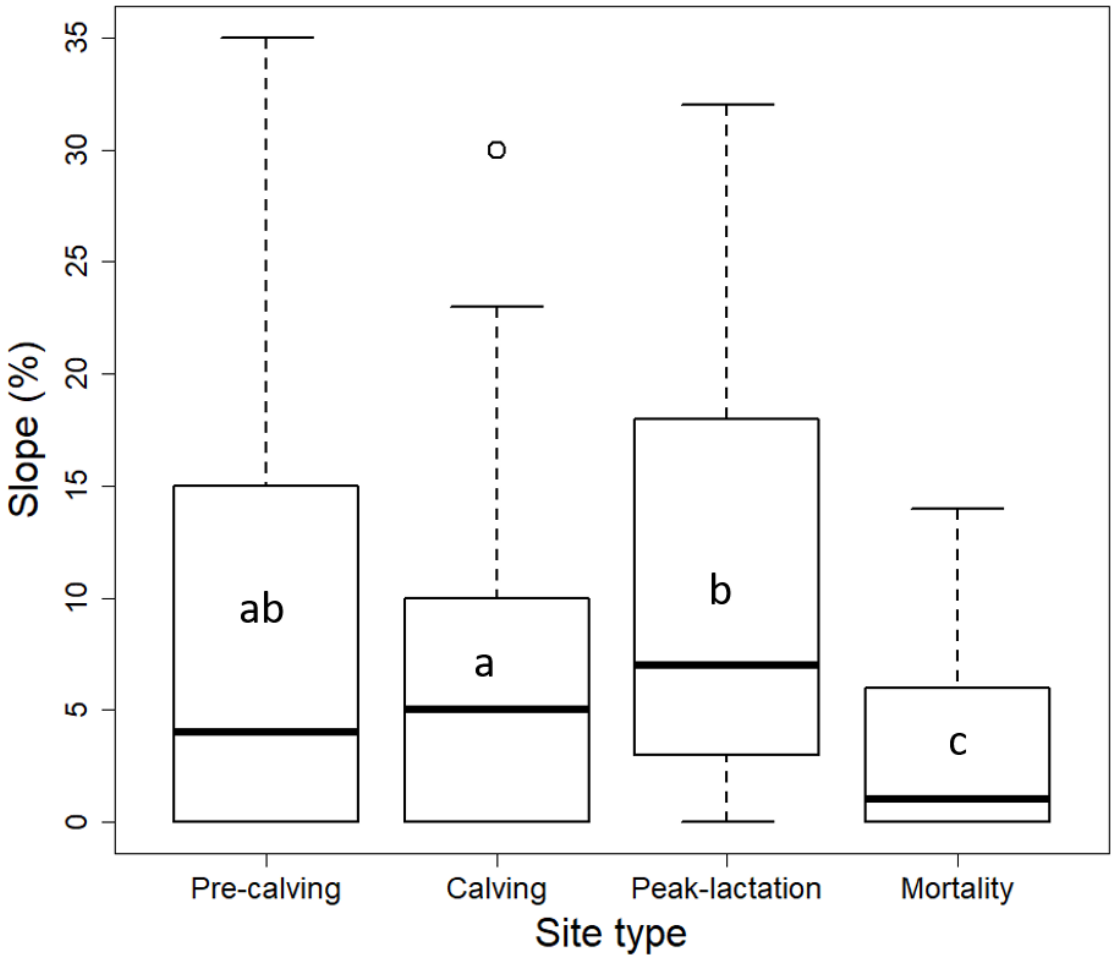

Figure 2. Prevailing slope (%) at pre-calving, calving, peak-lactation, and mortality sites (*n* = 34, 37, 25, and 10, respectively) of moose calves, May–July 2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range. Different letters depict a significant difference ($P < 0.05$).

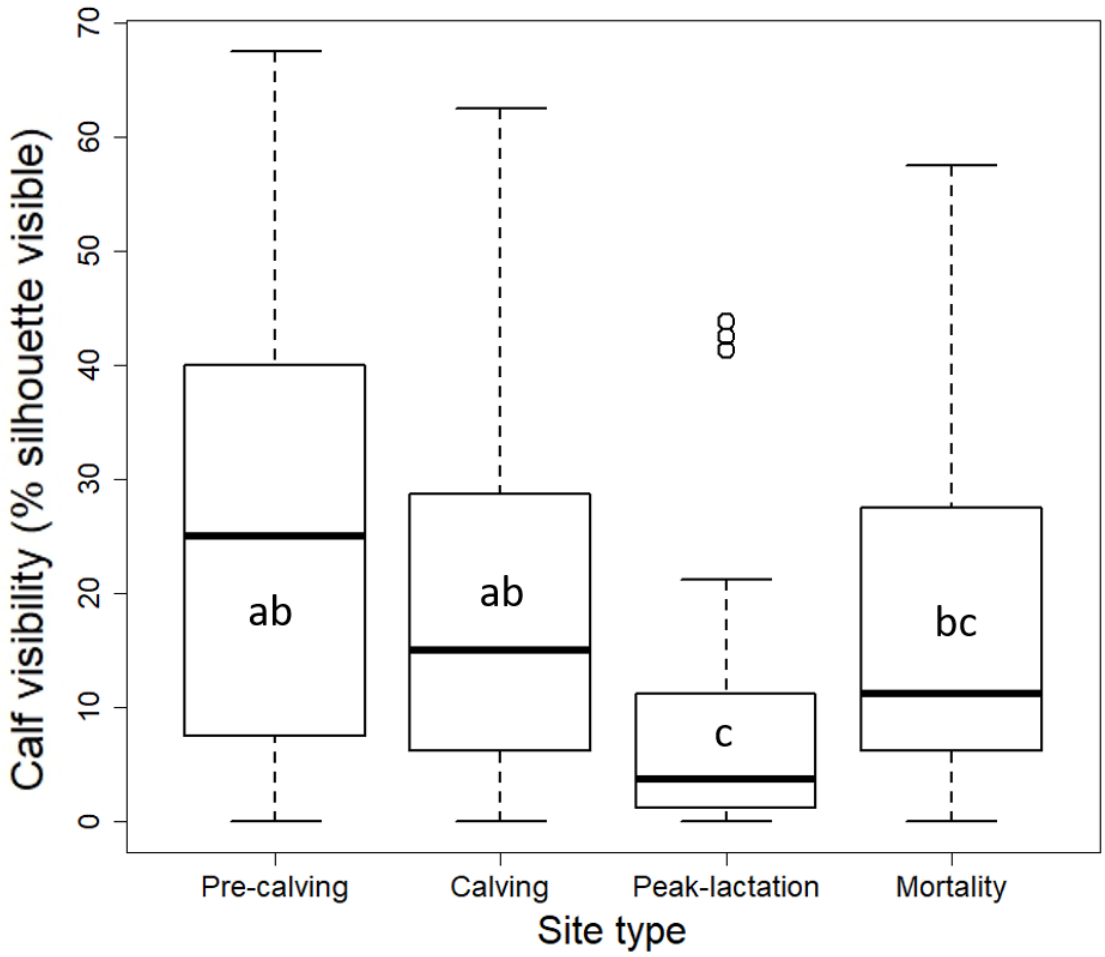

Figure 3. Calf visibility (percentage of calf silhouette visible from 15 m) at pre-calving, calving, peak-lactation, and mortality sites (n = 34, 37, 25, and 10, respectively) of moose calves, May–July 2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range. Different letters depict a significant difference (P <0.05).

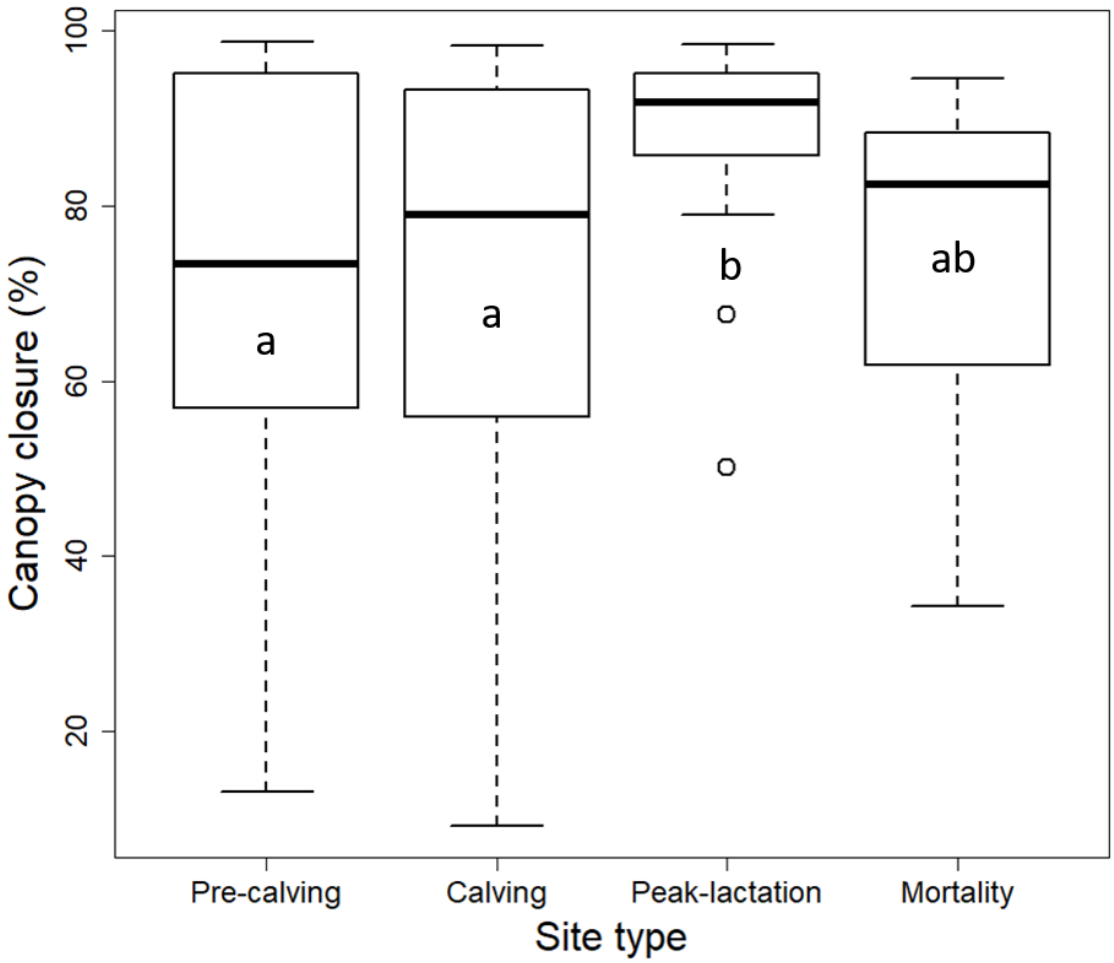

Figure 4. Mean canopy closure (%) at pre-calving, calving, peak-lactation, and mortality sites (n = 34, 37, 25, and 10, respectively) of moose calves, May–July 2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range. Closure measured using spherical crown densiometer at focal point plus 15 m from point in each cardinal direction. Different letters depict significant differences (P <0.05).

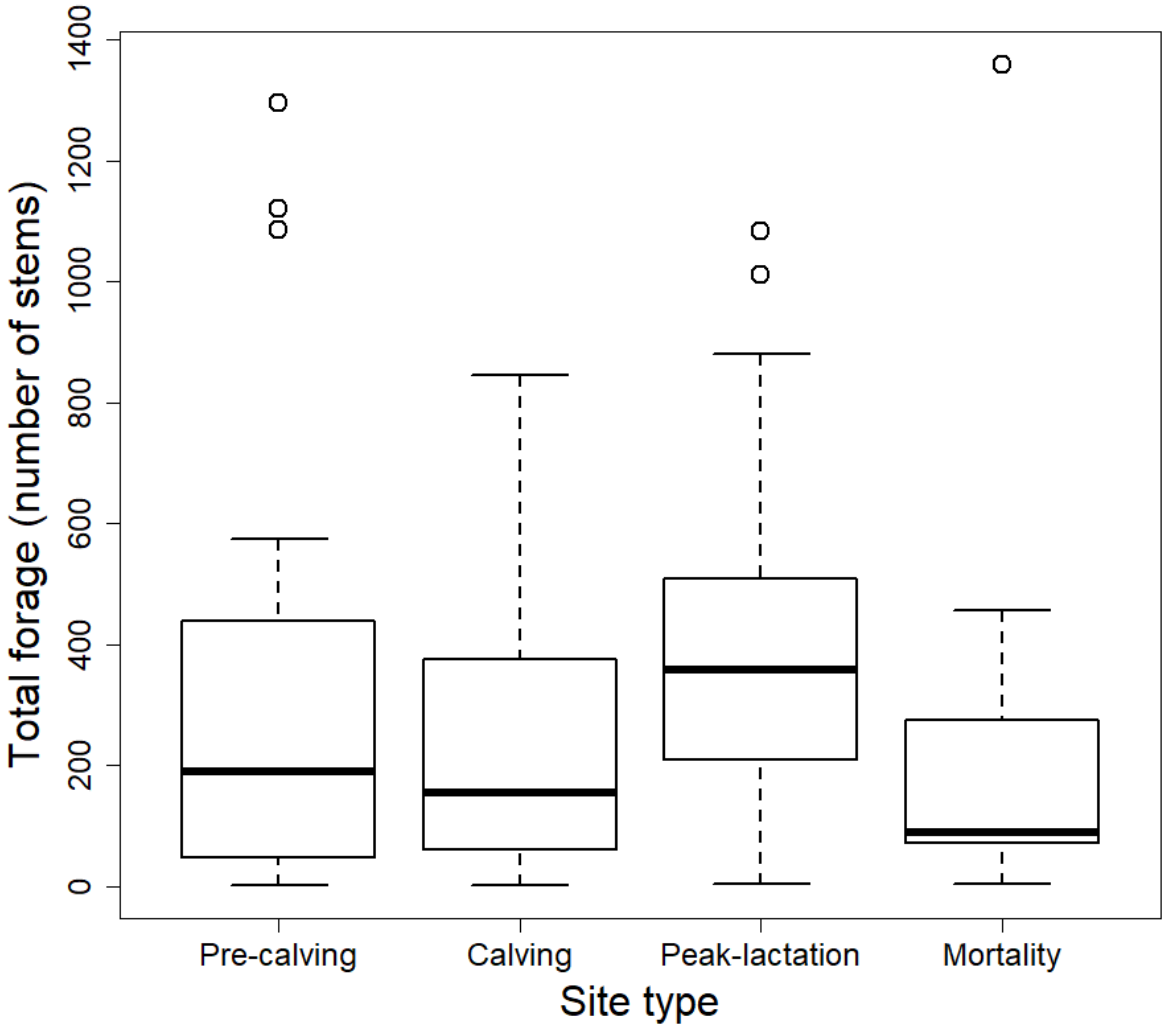

Figure 5. Forage (number of forage species stems <18 cm DBH) at pre-calving, calving, peak-lactation, and mortality sites (n = 34, 37, 25, and 5, respectively) of moose calves, May–July 2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range. Forage species were defined according to Peek et al. (1976) and Portinga and Moen (2015).

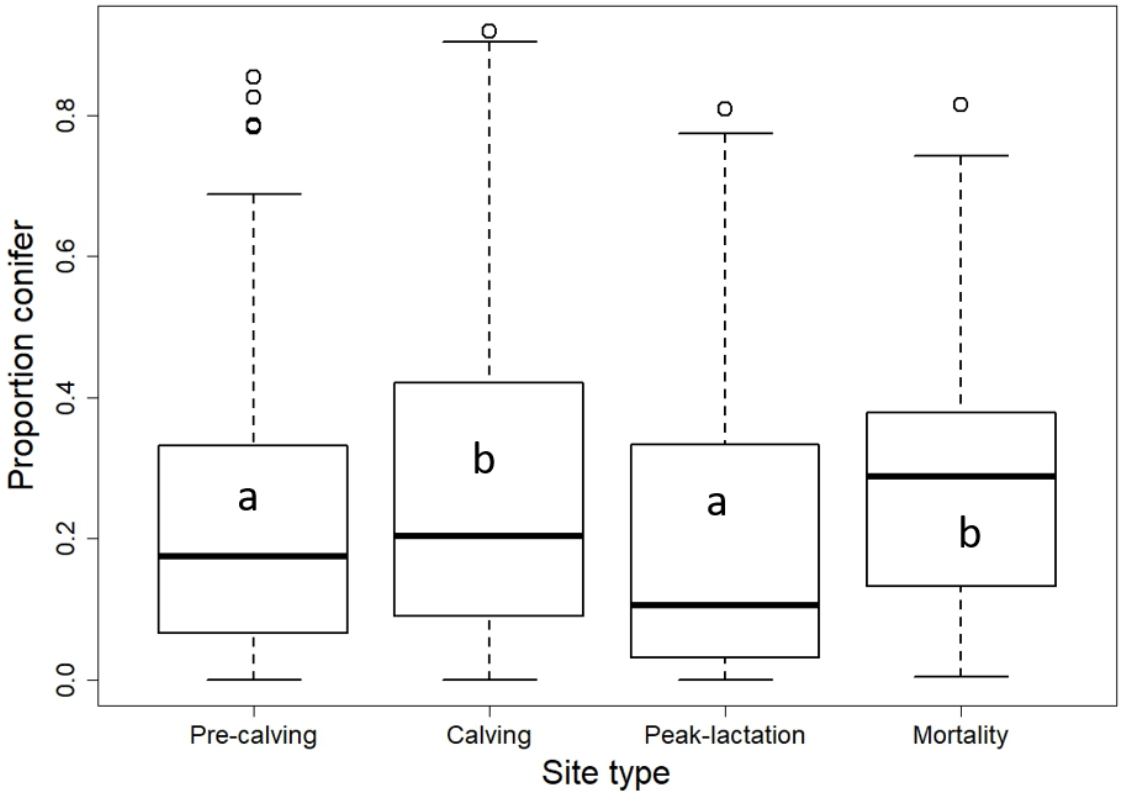

Figure 6. Proportion of 100-ha buffers of conifer forest cover type at pre-calving, calving, peak-lactation, and mortality sites (n = 150, 155, 73, and 36, respectively) of moose calves, May–July 2013–2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range. Different letters depict significant differences (P <0.05).

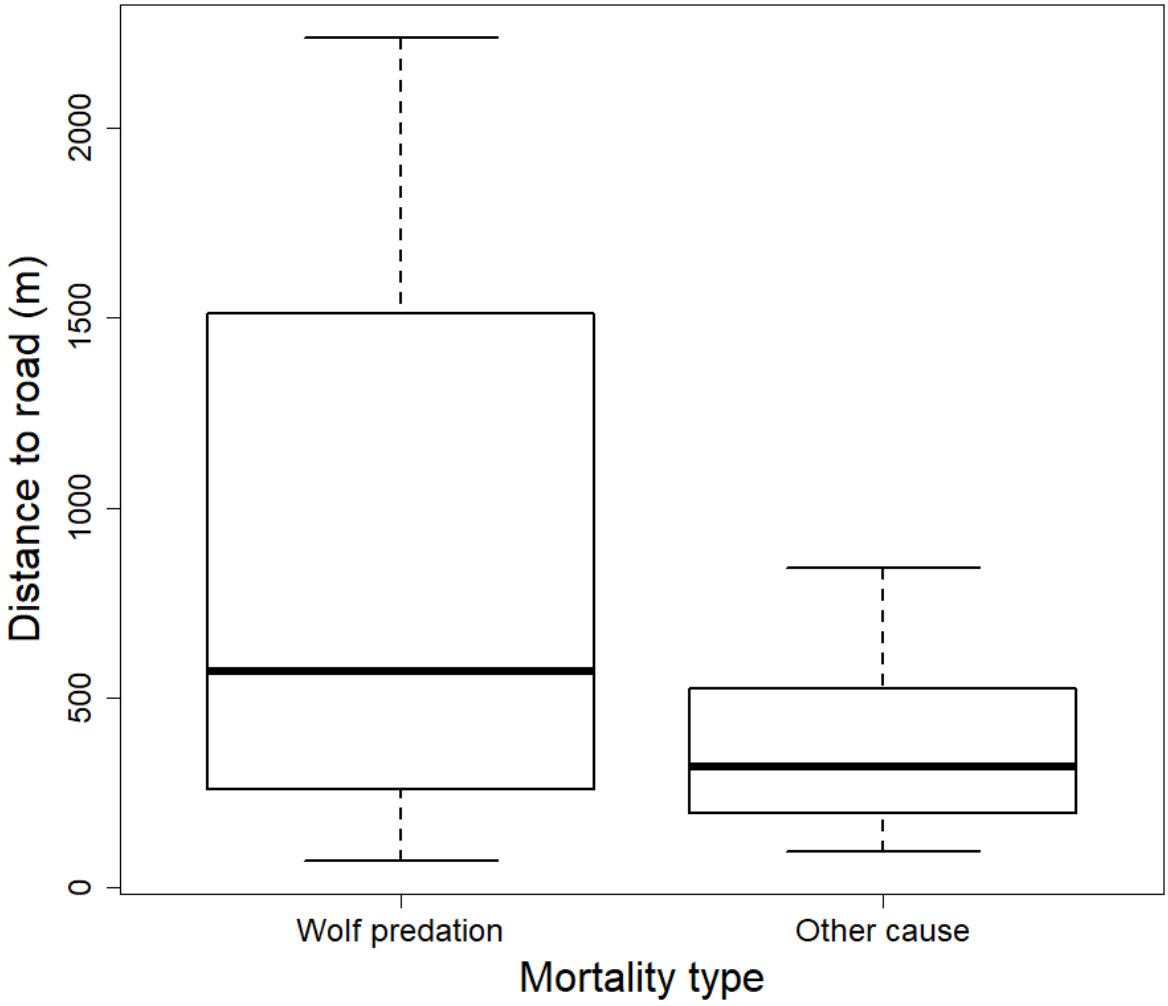

Figure 7. Distance to nearest road (m) at mortality sites of moose calves that were preyed upon by wolves ("Wolf predation", *n* = 24) and succumbed to other causes of mortality ("Other cause", *n* = 12; bear predation, unknown predation, drowning, natural abandonment, infection), May–July 2013–2015, northeastern Minnesota. Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are 1.5× interquartile range.

Chapter 4: Growth Rates and Population Projections of Northeastern Minnesota's Moose Population

ABSTRACT Long-term, the northeastern Minnesota moose (*Alces alces*) population has declined 58% since 2006, yet aerial survey estimates indicate stability during 2012–2017. In response to the initial decline, the Minnesota Department of Natural Resources initiated aggressive studies of adult and calf survival. The population has been consistently surveyed each winter using a standardized methodological approach since 2005. My objective was to estimate population growth rate (λ) using adult survival and calf recruitment data from the demographic studies and the Recruitment-Mortality (R-M) Equation, and to compare these estimates to those calculated using data from the aerial survey. I then projected population dynamics 50 years using each calculation method, and also used a stochastic model to project population dynamics 30 years using median and standard deviation of survival and litter size obtained from the demographic studies. Measures of recruitment were similar whether derived from the survey or collaring studies, but were generally higher in the collared sample. More recent calculations of λ (derived from the survey [2012–2017; 1.02 ± 0.16 (SE)] and using the R-M Equation [1.04 ± 0.04]) indicated growth over the next 50 years. However, the stochastic model using parameters from the adult and calf studies indicated an average decline in the population over the next 50 years (λ = 0.91 ± 0.004). The R-M Equation has utility, but supporting information from demographic collaring studies helps to further address management questions. Furthermore, estimates of λ calculated using collaring data were less uncertain and more reflective of current conditions. Long-term monitoring using

collars would better inform population performance predictions and demographic responses to environmental variability.

INTRODUCTION

Minnesota's northeastern moose (*Alces alces*) population has decreased 58% from a high point estimate of 8,840 in 2006 to 3,710 in 2017, but appears to have stabilized during 2012–2017 (DelGiudice 2017). Minnesota's northwestern moose population declined in a stair-step fashion from about 4,000 moose to <100 animals during 1980−2007 (Murray et al. 2006, Lenarz 2007). During the northwestern decline, average pregnancy rates (<50%) and adult female survival were low (79%), but calf survival was high (66%; Murray et al. 2006). A study of northeastern population demographics in 2002–2008 predicted a slow reduction in numbers (long-term stochastic growth rate of 0.85); modeled adult survival rates were 0.74–0.85 and calf survival was 0.24–0.56 (Lenarz et al. 2010). However, the decline was not indicated by the annual surveys until 2010 (ArchMiller et al. in press, Lenarz et al. 2010, DelGiudice 2013). Demographic modeling can reveal population trajectories before they are reflected in total population estimates.

In response to the precipitous decline in the northeastern population, the Minnesota Department of Natural Resources (MNDNR) initiated aggressive studies on adult and calf moose survival and cause-specific mortality in 2012. These studies built upon previous research of Lenarz et al. (2009, 2010), but the aims were to better understand the mechanisms (i.e., causes of mortality) behind the population dynamics (Butler et al. 2011, DelGiudice et al. 2012). The survival and cause-specific mortality studies used state-of-the-art global positioning system (GPS) collars and other remote

monitoring techniques to track survival, habitat use, cause-specific mortality, and physiological conditions (DelGiudice et al. 2015; Severud et al. 2015*a*, 2017; Carstensen et al. 2017; Herberg 2017; Obermoller et al. 2017).

Estimating population trends, identifying and understanding underlying mechanisms of change are important to wildlife management, but can be challenging pursuits. The MNDNR's moose survey yields useful demographic information regarding the northeastern moose population. Similarly, the survival and cause-specific mortality studies have been gaining detailed information about the mechanisms behind varying demographics. Due to resource limitations, agencies often cannot do both concurrently. Estimating adult and juvenile survival is difficult and costly, whereas population composition surveys may yield some comparable information at a lower cost. Hatter and Bergerud (1991) formulated the Recruitment-Mortality (R-M) Equation, that can readily employ survey data to calculate population rate-of-change and adult mortality rates. It is a rearrangement of $\lambda = N_1/N_0$, where $\lambda = (1 - \text{mortality})/(1 - \text{recruitment})$. Recruitment is defined as the calf proportion of the population at the time of survey (usually mid- to late-winter). The equation has been employed when 2 of the 3 parameters are known to solve for the unknown parameter and to compare growth rates derived from various other means (Hatter and Bergerud 1991, DeCesare et al. 2012, Serrouya et al. 2017).

My goal was to compare estimates of λ derived from demographic rates generated from the adult moose and calf studies versus the annual aerial surveys. I then projected population dynamics for 50 years to gauge how current trends may affect the population's future. I further compared projections calculated using research-derived

parameters to annual survey-derived parameters and examined the sensitivity of all parameters to determine which data may be most important to predicting growth. To model how variability in demographic rates may affect trajectories, I also used a stochastic model to project the population for 30 years using median and standard deviations of adult survival and litter sizes generated from the research.

STUDY AREA

The demographic studies and aerial surveys were conducted in northeastern Minnesota along the southern extent of moose range in North America (Lenarz et al. 2010, Timmermann and Rodgers 2017). This population of moose inhabits a mosaic of the Superior National Forest and various state, county, and private lands (6,068 km^2) between 47°06'N and 47°58'N latitude and 90°04'W and 92°17'W longitude. Moose harvest was suspended there from 2013 until 2016, when a limited tribal harvest was resumed (DelGiudice 2012). This region is part of the Northern Superior Upland within the Laurentian mixed forest province (MNDNR 2015). The vegetative cover is a mixture of wetlands, and lowland and upland stands of conifers. The uplands also contain deciduous species within the conifer stands. Timber harvest declined from 2001 to 2013 (Wilson and Ek 2013).

Predators of moose calves were gray wolves (*Canis lupus*) and American black bears (*Ursus americanus*; (Lenarz et al. 2009; Patterson et al. 2013; Severud et al. 2015*a*, *b*); wolf and bear densities were estimated at 4.4/100 km^2 and 23/100 km^2, respectively (Mech et al. in press, Garshelis and Noyce 2011). White-tailed deer, managed at pre-fawning densities of <4/km^2, were primary prey of wolves in the area (Nelson and Mech

1981, DelGiudice et al. 2002, MNDNR 2012). Alternate wolf prey included beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), black bears, and various small mammals (Stenlund 1955, Frenzel 1974, Van Ballenberghe et al. 1975, Chenaux-Ibrahim 2015).

METHODS

Aerial Surveys

The MNDNR conducts an aerial survey of the northeastern moose population each winter (DelGiudice 2017). The survey estimates abundance (including 90% CI), percent calves, calf:cow and bull:cow ratios, and percent cows observed with twins. A sightability model corrects for visual obstruction and is used to adjust abundance (ArchMiller et al. in press, Steinhorst and Samuel 1989, Fieberg 2012, Giudice et al. 2012), but raw data are used to calculate other metrics.

Adult and Calf Survival Rates

Adult moose were captured, handled, and fitted with GPS collars 2013–2015 (Carstensen et al. 2017). Calves were monitored for survival 2013–2015, but were fitted with GPS collars in 2013 and 2014 only (Severud et al. 2017). Adult females were blood-sampled to test for pregnancy; a threshold of ≥2 ng/mL indicated pregnancy (Haigh et al. 1982, Testa and Adams 1998, Murray et al. 2006). Annual survival was calculated for pooled adult (>1.5 yr) males and females and for calves (birth to 1 yr) during 2013–2016. Kaplan-Meier survival rates were estimated using *KMsurv* in R (R Core Team 2017). Survival rates were published elsewhere (Carstensen et al. 2017, Obermoller et al. 2017, Severud et al. 2017).

Calculation of Lambda (λ)

I calculated λ using 2 different methods. First, to calculate λ_{survey} I used population estimates from the annual aerial survey and the equation:

$$\lambda_{survey} = (\frac{N_t}{N_0})^{(1/t)}$$

where *N* was the population estimate and *t* is the time interval between surveys.

Second, I used the Recruitment-Mortality (R-M) Equation (Hatter and Bergerud 1991) to calculate $\lambda_{R\text{-}M}$:

$$\lambda_{R-M} = \frac{(1 - M)}{(1 - R)}$$

where *M* is the finite annual adult mortality rate and *R* is the finite annual recruitment rate defined as the calf proportion of the population. I used published adult survival estimates (S_{adult}) to calculate mortality using $1 - S = M$ (Carstensen et al. 2017). To obtain estimates of *R* I used the population estimate, bull:cow ratio (DelGiudice 2017), mean twinning rate (M. Schrage, Fond du Lac Resource Management Division, unpublished data), pregnancy rates, and annual calf survival from GPS-collared and uncollared calves (Obermoller et al. 2017, Severud et al. 2017). Pregnancy rates were estimated using GPS-collared cow information from captures (serum progesterone) and subsequently from "calving movements" and cows observed with calves. I used estimates from the year prior to calculate the current year's *R* (e.g., 2013 population estimate, bull:cow ratio, pregnancy rate, and calf survival to calculate 2014's *R*). First, I calculated calf production as:

$$calf\ production$$

$$= (pop'n\ estimate\ \times\ proportion\ cows\ \times\ preg\ rate)$$

$$+ (pop'n\ estimate\ \times\ proportion\ cows\ \times\ preg\ rate$$

$$\times\ twinning\ rate)$$

I then used calf survival to calculate R as:

$$R_{study\ t} = \frac{calf\ survival_{t-1}\ \times\ calf\ production_{t-1}}{pop'n\ estimate_{t-1}}$$

M can also be calculated by rearranging the R-M Equation into:

$$M = 1\ -\ \lambda(1\ -R)$$

Using this equation, I estimated adult mortality rates from λ_{survey} and R_{survey} to compare how closely they tracked to mortality rates observed in the demographic study.

Population Projection

I calculated median and standard deviation of S_{adult} and calf:cow ratios at calving (litter size). I then used the 2014 population estimate for the initial population (4,350 adults) and projected growth for 30 years and 100 Monte Carlo simulations using the R package *population* (Chapron 2015). I also projected the population for 50 years using mean λ_{survey} from the recent stable period (2012–2017) and from the entire period (2005–2017), mean $\lambda_{R\text{-}M}$, and the long-term stochastic growth rate from a previous study (0.85; Lenarz et al. 2010). I investigated sensitivity of all parameters used to calculate $\lambda_{R\text{-}M}$ by incrementally increasing a single parameter while holding the others at mean levels until λ increased from 1.00 to 1.10.

RESULTS

The MNDNR collared 173 adult moose from 2013 to 2015 (123 F, 50 M) to track survival and cause-specific mortality (Carstensen et al. 2017). Survival was pooled for males and females due to a small sample of males. Reported adult annual survival estimates for 2013–2016 were 0.81, 0.88, 0.86, and 0.85, respectively (Carstensen et al. 2017). Seventy-four neonates were collared in 2013 and 2014 (combined), with an additional 103 uncollared calves of GPS-collared dams monitored for survival in 2015 (n = 65) and 2016 (n = 38). Estimated annual calf survival rates were 0.28, 0.40, 0.40, and 0.33, for 2013–2016, respectively (Obermoller et al. 2017, Severud et al. 2017).

The aerial survey reported population estimates, calf:cow ratios, percent of the population composed of calves, percent of cows observed with twins, and bull:cow ratios (DelGiudice 2017). I estimated pregnancy rates of 0.74, 0.81, 0.88, and 0.89 for 2013–2016, respectively. I used a mean twinning rate of 30% (M. Schrage, Fond du Lac Resource Management Division, unpublished data). Mean R_{study} was 0.18 (range = 0.12–0.23), whereas mean R_{survey} for the same time period was 0.15 (range = 0.13–0.17; Table 1). R_{survey} and R_{study} closely tracked each other for all years except 2016 (Fig. 1), with a general pattern of R_{study} being slightly higher.

I calculated mean λ_{survey} for 3 different periods based on a piecewise polynomial that indicated the population has gone through 3 distinct periods: stability (2005–2009), decline (2009–2012), and then stability again (2012–2017; DelGiudice 2017). The initial stable period λ_{survey} was 1.00, followed by 0.82 during the decline, and then 1.02 during the current stable period. The highest λ_{survey} for a single year was 2014 (1.58), when the population estimate increased dramatically after an extremely low population estimate in

2013 (Fig. 2). Similarly, the lowest estimate of λ_{survey} was in 2013 (0.65) when the population dropped markedly (Table 1).

Mean $\lambda_{R\text{-}M}$ for 2014–2017 was 1.04 (±0.04 [SE], range = 0.92–1.12, n = 4), indicative of a slightly growing population, and similar to estimates of λ_{survey} during the current stabilization (1.02 ± 0.16; 2012–2017). The highest observed $\lambda_{R\text{-}M}$ was 1.12 for 2016 (Table 1), when both adult mortality was relatively low (14%) and previous year's calf survival was high (40%). Pregnancy rate was also high (0.88). Using the 2013 population estimate as a common starting point, I used $\lambda_{R\text{-}M}$ to project population for 2014–2017 (Fig. 3). The modeled projection closely matched the observed estimates (within 90% confidence intervals) except for 2014, when $\lambda_{R\text{-}M}$ was lower than the population estimate. Adult mortality rates widely varied, but the mean during 2013–2017 was 13.0% which is similar to the adult study average of 13.8%. However, the R-M Equation calculated a negative mortality rate in 2014 (−34%).

Holding all other parameters at mean rates (S_{adult} = 0.85, twinning rate = 0.30, pregnancy rate = 0.83, proportion cows = 0.48, mean population = 5,593), an increase of S_{calf} from 0.285 to 0.435 (0.15 difference) increased $\lambda_{R\text{-}M}$ from 1.00 to 1.10. However, if S_{calf} is held constant at 0.285, an increase from 0.850 to 0.935 (0.085 difference) in S_{adult} results in the same change in λ. A similar increase of λ from 1.00 to 1.10 would require the bull:cow ratio to change to 75% cows or increasing twinning rate to 100%. A 100% pregnancy rate would only increase λ from 1.00 to 1.03.

Deterministic projections using mean λ_{survey} from the recent stable period (2012–2017; 1.02) resulted in a growing population (Fig. 2). Using λ_{survey} from 2005–2017

(0.96) resulted in a slowly declining population. Mean λ_{study} (1.04) resulted in a dramatic increase in population over 50 years. The matrix projection from Lenarz et al. (2010; 0.85 from 2002–2008) indicated a declining population, yet survey results have been above the trajectory for 2014–2017. The stochastic model using median demographics (adult survival = 0.85 ± 0.03 [SD], cow:calf ratio at birth = 1.12 ± 0.32) from the MNDNR studies shows the population slowly declining, but with uncertainty ($\lambda = 0.91 \pm 0.04$; Fig. 4).

DISCUSSION

Population dynamics are difficult to determine for cryptic, typically solitary, forest-dwelling species. The R-M Equation is a method to estimate λ without age-specific survival and fecundity rates needed for more intensive modelling. I projected the northeastern Minnesota moose population using 3 calculations of λ and one from the literature (Lenarz et al. 2010). Two of these projections predicted an increasing population and 2 indicated a decreasing trend. The increasing trajectories used more recent estimates of λ (2012–2017 survey-derived and 2014–2017 study-derived). The stochastic projection resulted in a slowly decreasing population. These estimates of λ are reflective of more current conditions (environmental, demographic), which may change through time and increase standard errors in predictions (Ellner and Fieberg 2003). Environmental fluctuations, such as those associated with climate change, will likely alter species distributions and abundance. Range shifts may be a more severe outcome over a long time scale, whereas decreases in density may result at shorter time scales (Ehrlén and Morris 2015). Climate change, specifically warming temperatures, are expected to

influence moose demographics at the southern periphery of their geographic range (Murray et al. 2006; Lenarz et al. 2009, 2010; McCann et al. 2013; but see Mech and Fieberg 2014). The northeastern Minnesota moose population has shown some response to warmer than average winter temperatures, including reduced survival (Lenarz et al. 2009, but see Mech and Fieberg 2014) and an increase in winter nutritional restriction (DelGiudice and Severud 2017). Similarly, behavioral changes (e.g., use of habitat) in response to warm temperatures have been observed (McCann et al. 2016, Street et al. 2016).

Estimates of λ calculated from survey data varied widely from 0.65 to 1.58, whereas λ calculated using the R-M Equation from the adult and calf demographic studies ranged from 0.92 to 1.12. The extreme values of λ from the survey are both influenced greatly by the extremely low 2013 population estimate. This point estimate was associated with poor survey conditions, and consequently, has been considered an outlier (G. DelGiudice, MNDNR, personal communication). The large variation also underscores that the survey should be used to assess long-term trends rather than year-to-year changes in the population. Growth rates calculated from the adult and calf studies suggest that the northeastern Minnesota moose population is slowly growing (about 4% per year). The λ_{survey} associated with the stability of 2012–2017 is similar to estimates from the R-M Equation (1.02 vs. 1.04). Although the point estimates of the annual survey do not appear to reflect an increase in total population, there could potentially be a time lag. Lenarz et al. (2010) reported declining population projections despite the

annual survey not yet revealing the decline, suggesting that a large increase in the population may be required before a significant change in the point estimates is observed.

Varying adult survival had more of an impact on λ than varying calf survival or any other parameter contributing to *R* in the R-M Equation (twinning rate, pregnancy rate, bull:cow ratio). Lenarz et al. (2010) similarly concluded that fertility, calf survival, and adult survival explained 5, 11, and 70% of the variation in λ, respectively. Large herbivore adult survival is generally high and more consistent than juvenile survival (Gaillard et al. 1998, 2000), so low and highly variable calf survival can greatly impact population dynamics (Raithel et al. 2007, Lenarz et al. 2010). The demographic studies showed adult survival rates have been stable relative to calf survival (standard errors of 0.01 versus 0.03). The range of observed calf survival has been 0.28 to 0.40. If calf survival were consistently nearer 0.40, then the population could possibly grow (i.e., λ >1). Adult survival has more potential to influence λ, but it is already fairly high and constant. Management strategies and activities aimed at markedly altering other parameters such as bull:cow ratios, twinning rates to 100%, and pregnancy rates are not likely feasible and would not have much impact on λ. The population is already near its maximum reproductive output.

My calculations of R_{study} closely tracked R_{survey}, but because there are assumptions (e.g., twinning rate) and uncertainty (calf survival) surrounding parameters used to calculate R_{study}, it should be interpreted cautiously. The largest disparity between R_{study} and R_{survey} occurred in 2016, which was dependent upon 2015 calf survival estimates. In April 2015, the governor of Minnesota issued an executive order barring collaring of

moose in the state. Instead of collaring neonates as planned, new methods were developed to monitor calf survival. Because this was the first time these methods were developed and implemented, the survival estimate warrants prudent interpretation. Furthermore, methods used to estimate recruitment in all years of the calf-survival study may have missed late-winter mortality observed elsewhere (Musante et al. 2010, Jones et al. 2017, Serrouya et al. 2017).

To estimate population demographics, a large and geographically dispersed sample of that population is followed to ensure the sample is representative. The MNDNR collared large numbers of adult and calf moose across the study area. Whereas the goal was to maintain about 100 animals transmitting for the duration of the study, the executive order plus attrition of existing collars due to mortalities and battery-life expiration greatly reduced sample size (Carstensen et al. 2017). The adult mortality rate has generally been decreasing, but later estimates could be biased due to weakened animals being culled from the population through predation or health-related mortality and stronger animals surviving to later years of the study. A relationship between collared adult survival rates and population-wide assessments of winter nutritional restriction suggests the condition of the collared animals has been representative of that of the free-ranging population in the earliest years of the study (DelGiudice and Severud 2017). The R-M Equation is elegant in that it does not require age-specific survival or fecundity data (Hatter and Bergerud 1991). If collaring demographic studies can no longer be conducted in Minnesota, λ, R, and M can be estimated via the annual aerial survey; however, λ and M can be influenced by wide fluctuations in the population point

estimate, as was seen before and after 2013. After the large increase from 2013 to 2014, an artifact of survey condition in 2013, a negative mortality rate was observed, as was seen in other rapidly increasing populations (Hatter and Bergerud 1991). An integrated population model using survey estimates combined with demographic data from the MNDNR studies may be another method to better understand trends in the population (Besbeas et al. 2002). Reliance solely upon the survey to understand moose population dynamics will not be as informative or useful in the absence of demographic data gained from collaring studies (Murray 2006, Berg et al. 2017). Thus, the biologically significant value of resumed collaring cannot be overstated.

MANAGEMENT IMPLICATIONS

Aerial survey results indicate that the population was stable during 2012–2017, and population modeling suggests that the population may have increased in the short-term; however, over the long-term, models made varying predictions about the direction of population trajectory. With collaring no longer possible to track the population, *R* and *M* can still be estimated from the survey. The parameter *R* integrates fecundity and calf survival, but cannot give information on timing and cause of mortality or twinning rates, all which are of keen interest and value to management. Estimates of *M* can be unrealistic given the low precision of the population estimate. The R-M Equation has utility, but supportive information from demographic collaring studies helps to further address management questions.

Table 1. Demographic parameters of moose derived from annual aerial surveys and studies of adult and calf survival, 2013−2017, northeastern Minnesota. *N* is the population estimate, *M* is the annual adult mortality rate, *S* is calf survival, *R* is recruitment (calf proportion of the population), and preg rate is pregnancy rate as determined by serum progesterone, calving behavior, and calf observations. λ_{survey} was calculated using changes in population estimates; $\lambda_{R\text{-}M}$ was calculated using the R-M Equation, $(1-M)/(1-R)$.

Survey year	N[a]	M_{adult}[b]	S_{calf}[c]	R_{survey}[a]	R_{study}[c]	Preg rate	Calf production	λ_{survey}	$\lambda_{R\text{-}M}$
2013	2,760	0.19	0.28	--	--	0.74	1,196	0.65	--
2014	4,350	0.12	0.40	0.15	0.12	0.81	2,056	1.58	0.92
2015	3,450	0.14	0.40	0.13	0.19	0.88	1,991	0.79	1.09
2016	4,020	0.15	0.33	0.17	0.23	0.89	2,280	1.17	1.12
2017	3,710	--	--	0.15	0.18	0.85	2,146	0.92	1.04
Mean		0.15	0.35	0.15	0.18	0.83	1,934	1.02	1.04
SE		0.01	0.03	0.01	0.02	0.03	191	0.16	0.04

[a]DelGiudice 2017.

[b]Carstensen et al. (2017), M. Carstensen (MNDNR, personal communication).

[c]Severud et al. (2017), Obermoller et al. (2017).

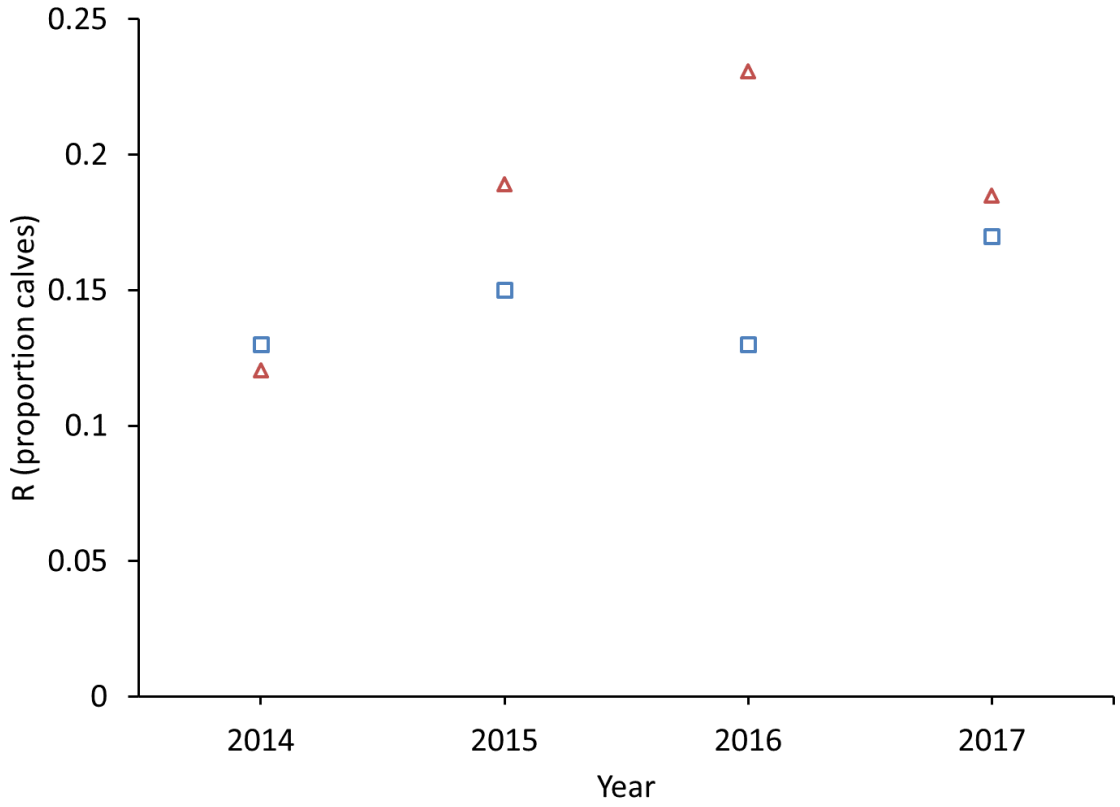

Figure 1. Estimated recruitment (*R*; calf proportion of the total population) observed during the annual aerial survey (squares; R_{survey}; DelGiudice 2017) and calculated using parameters from calf survival study (triangles; R_{study}; Severud et al. 2017, Obermoller et al. 2017), 2014–2017, northeastern Minnesota.

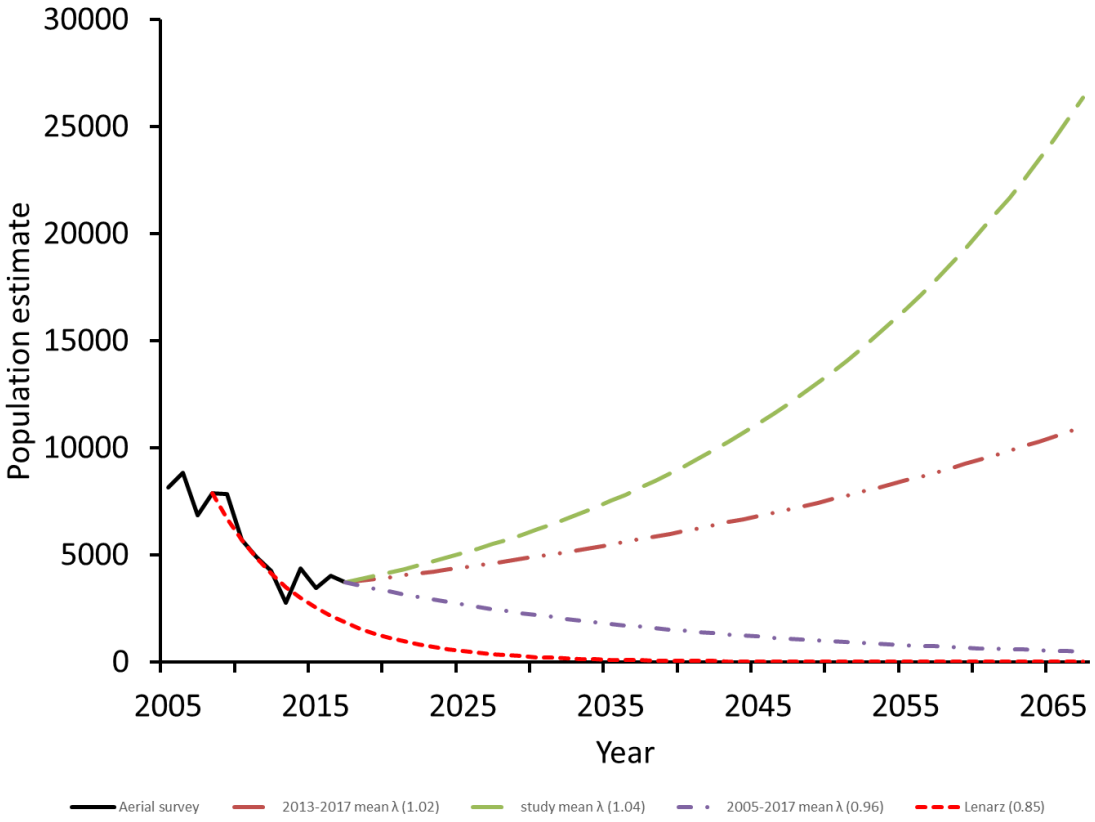

Figure 2. Northeastern Minnesota moose population estimates (2005–2017) with deterministic projections using 3 calculations of λ from 2017 onward, and 1 projection from 2008 onward (λ = 0.85 from Lenarz et al. 2010).

Figure 3. Northeastern Minnesota moose population estimate (solid black line) plus 90% confidence intervals (dashed black lines) during the 2012–2017 apparent stabilization (DelGiudice 2017), and modeled population (solid red line) plus standard error (dotted red line) using $\lambda_{R\text{-}M}$ from 2013 onward.

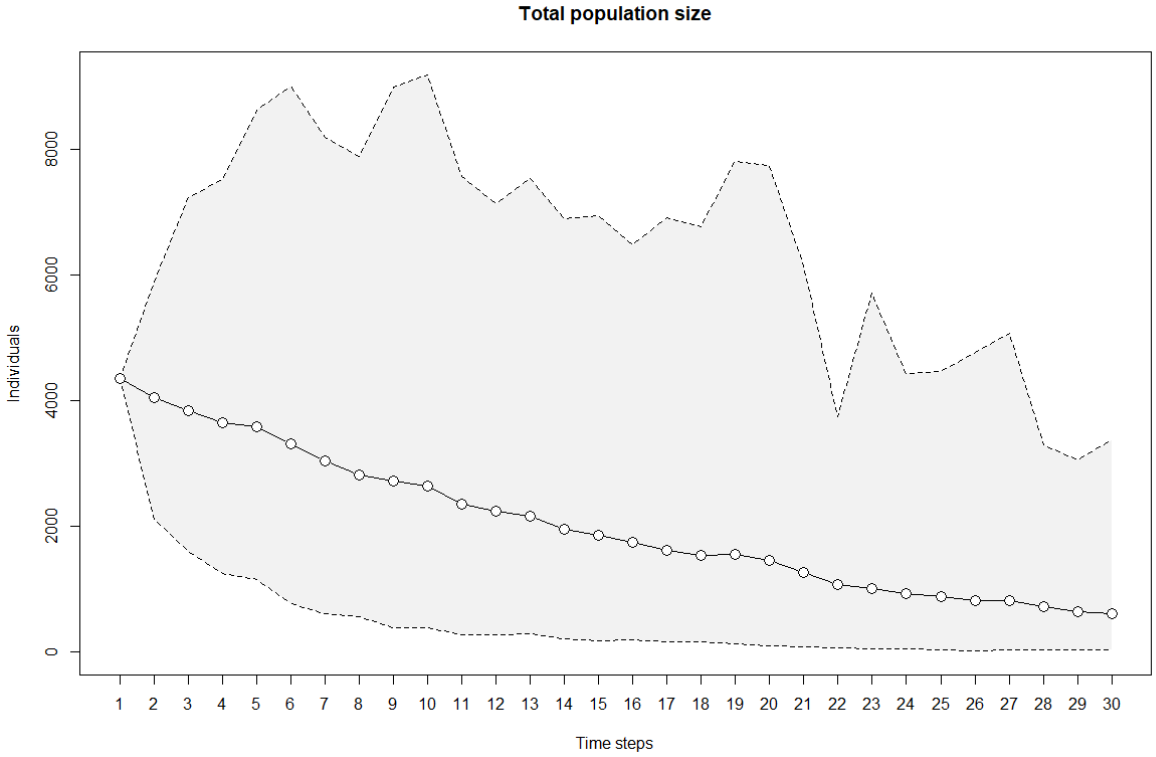

Figure 4. Stochastic population projection (30 yr) of moose in northeastern Minnesota from 2014 (N = 4,350) onward using median ± standard deviation of adult survival (0.85 ± 0.04) and litter size (calf:cow ratio at birth, 1.12 ± 0.32). Shaded area represents limits from 100 Monte Carlo simulations using the R package *population*.

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